# PART V

# GRAPTOLITHINA

## WITH SECTIONS ON ENTEROPNEUSTA AND PTEROBRANCHIA

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## CONTENTS

# INTRODUCTION

This section of the *Treatise* is concerned essentially with the Graptolithina, but it is prefaced with a short account of living and fossil Hemichordata (*Balanoglossus, Cephalodiscus,* and *Rhabdopleura*). The reason for this is that although the graptolites are an extinct group, confined to the Paleozoic, morphological discoveries during the past 20 years have made it seem probable that they may be allied more nearly to some of the Hemichordata than to any other living group, and accordingly they are here provisionally regarded as a separate class of that phylum. An account of morphology of the soft parts, particularly of *Rhabdopleura,* may therefore help the student to visualize the kind of zooid which probably inhabited the graptolite rhabdosome, though it must be borne in mind that the analogy is tentative. The evidence concerning graptolite affinities is discussed here on p. *V*22 and the broader classification of these living protochordates adopted here accords with that used by BARRINGTON (1965), where also will be found a concise discussion of the relations of the protochordates to other Deuterostomia.

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All figures have been specially drawn and are "after" rather than "from" the sources indicated.

# GENERAL FEATURES

While the tunicates (Urochordata) and Acrania (Cephalochordata) are currently accepted as protochordate members of the phylum Chordata, the Hemichordata are now regarded by most authorities as constituting an independent phylum. It is extremely difficult, however, to give a concise, comprehensive survey of the general features of the varied and specialized groups comprised in this phylum. The Enteropneusta and Pterobranchia are virtually the only two living classes, for the Planctosphaeroidea scarcely merit consideration here, and the Graptolithina are an extinct class provisionally assigned to the phylum; the affinities of the Graptolithina and the nature of the graptolite zooid are discussed on p. *V*22.

The Enteropneusta lack any coenoecium (external skeleton) common to the other two classes, but show significant resemblances to the Pterobranchia in their soft-part morphology and ontogeny. The Graptolithina show significant coenoecial resemblances to the Pterobranchia, though their zooids are known only by inference. Thus the features linking the enteropneusts to the pterobranchs are inapplicable to the Graptolithina, and those connecting the Graptolithina and the Pterobranchia are irrelevant to the Enteropneusta.

The Enteropneusta and the Pterobranchia belong to the Deuterostomia because the anus develops from the blastopore and the mouth represents a new opening. Also they possess an enterocoelic coelom divided into anterior, median, and posterior chambers. As Hemichordata, they possess in addition pharyngeal openings (absent in *Rhabdopleura*), but they are distinct from the Chordata because they lack a notochord and an endostyle (an organ homologous with the thyroid gland of the Chordata). The body shows a division into proboscis or cephalic shield, collar, and trunk, and following metamorphosis of the tornaria larva, the larval pterobranch bears a strong resemblance to the wormlike enteropneusts, with a tripartite body and terminal anus.

The graptolithine and pterobranch coenoecium or rhabdosome consists of tubes, or thecae, which may comprise both fusellar and cortical tissue of scleroproteic composition and in at least some orders of both classes a comparable stolon system occurs. The external layer of living tissue postulated in the Graptolithina has no counterpart in any known pterobranch (or indeed in any other hemichordate).

# OUTLINE OF CLASSIFICATION

## HISTORICAL NOTES ON CLASSIFICATION OF GRAPTOLITHINA

The name *Graptolithus* was applied by LINNÉ in 1735 (*Systema Naturae,* edit. 1) to inorganic markings (such as dendritic incrustations) simulating fossils, and when in his 12th edition of *Systema Naturae* (1768) he included *G. sagittarius* and *G. scalaris,* these, too, were considered to be inorganic. The former nominal species is possibly a fossil plant, and the latter probably a graptolite. In his *Skånska Resa* (1751) he had described and figured a "Fossil or graptolite of a strange kind," now believed to represent *Climacograptus scalaris* and *Monograptus triangulatus;* and in 1821 the name *Graptolithus* was used by WAHLENBERG for definite graptolite remains. HISINGER, MURCHISON, and others described many more, and BRONN *(Index Palaeontologicus)* listed species known to him up to 1846, placing them in a subdivision of the Anthozoa. Numerous genera and subgenera came to be described during the second half of the century (see p. *V*100) and following LAPWORTH, 1873, the name *Graptolithus* was abandoned; it was formally suppressed in 1954 (ICZN, Opinion 197) and placed on the list of rejected generic names in view of the doubtful nature of the genolectotype and the originally-expressed intention to denote inorganic objects.

Several older writers had used some kind of key arrangement of genera in systematic sections of their work, and NICHOLSON (1872) in his uncompleted *Monograph* divided his family Graptolitidae into four "sections": Monoprionidae and Diprionidae for uniserial and biserial rhabdosomes (based on BARRANDE's "subgenera" *Monoprion* and *Diprion*), Tetraprionidae, and Dendroidea. This seems to be the first positive separation of the Dendroidea from the true graptolites and NICHOLSON wrote:

"These forms are very doubtfully referable to the Graptolitidae." The first formal classification into families was that of LAPWORTH, 1873, prefaced by a short but penetrating analysis of the structure and development of graptolite rhabdosome. To a remarkable extent this still constitutes the basis of current classification and it is quoted below:

### *Lapworth's (1873) Arrangement of Graptolite Rhabdosomes*

RHABDOPHORA (Allman)
Section I. GRAPTOLITIDAE
Family I. Monograptidae
Family II. Nemagraptidae (HOPKINSON MS)
Family III. Dichograptidae
Family IV. Dicranograptidae
Family V. Diplograptidae
Family VI. Phyllograptidae
Section II. RETIOLOIDEA
Family VII. Glossograptidae (provisional Family)
Family VIII. Retiolitidae

With renaming of the Nemagraptidae as Leptograptidae (LAPWORTH, 1879), merging of the Phyllograptidae in Dichograptidae, and addition of the Dimorphograptidae (ELLES & WOOD, 1908), together with the suppression of Section II, Retioloidea, we find virtually the classification used in the *Monograph of British Graptolites* (ELLES & WOOD, 1901-19). ALLMAN's term Rhabdophora, erected by him as a suborder of the Hydroida, became redundant when the Retioloidea were merged with the Graptoloidea, and HOPKINSON's comparable term Cladophora (HOPKINSON & LAPWORTH, 1875) is synonymous with Dendroidea (NICHOLSON, 1872).

Although WIMAN (1895), retained the "group" Retioloidea, he based the Dendroidea not only on the dendroid rhabdosome habit but, more important, on thecal polymorphism. In spite of this, the dendroids were again reduced to family rank by FRECH (1897), who included them with the Dichograptidi in his Axonolipa, distinguished from all other graptolites which constituted his Axonophora. This emphasis on the presence or absence of a virgula was, of course, quite excessive, for FRECH did not appreciate the identity of the virgula with the nema. Moreover, it is a feature difficult to apply systematically, and RUEDEMANN (1904, 1908) adopted the FRECH grouping but with a different familial composition. The terms Axonolipa and Axonophora are often useful adjectivally, but are not now accepted as having any taxonomic value.

Other families have been added to the Graptoloidea and the Dendroidea in recent years, and several new orders have been added to the Graptolithina by KOZŁOWSKI.

## CLASSIFICATION OF HEMICHORDATA

The following tabulation records numbers of genera in suprageneric divisions of Enteropneusta, Pterobranchia, and Graptolithina, accompanied by statements of stratigraphic ranges. Family-group taxa which contain subgenera are accompanied by two figures, the number of included genera being indicated by the first and subgenera additional to nominotypical subgenera by the second. Thus, the figures 16;1 indicate 16 genera and 1 subgenus in addition to the nominotypical one.

### *Main Divisions of Enteropneusta, Pterobranchia, and Graptolithina*

- Hemichordata *(phylum)*. (202;10). *M.Cam.-Rec.*
  - Enteropneusta *(class)*. (12). *Rec.*
  - Pterobranchia *(class)*. (7;3). *L.Ord.(Tremadoc)-Rec.*
    - Rhabdopleurida *(order)*. (3). *L.Ord.-Rec.*
      - Rhabdopleuridae (3). *L.Ord.-Rec.*
    - Cephalodiscida *(order)* (4;3). *L.Ord.(Tremadoc)-Rec.*
      - Eocephalodiscidae (1). *L.Ord.(Tremadoc).*
      - Cephalodiscidae (3;3). *Ord., ?Tert., Rec.*
  - Planctosphaeroidea *(class)*. *Rec.*
  - Graptolithina *(class)* (183;7). *M.Cam.-Carb.*
    - Dendroidea *(order)* (21;3). *?M.Cam., U.Cam.-Carb.(Namur.)*
      - Dendrograptidae (9;3). *?M.Cam., U.Cam.-Carb.*
      - Anisograptidae (11). *L.Ord.(Tremadoc), ?U.Ord.*
      - Ptilograptidae (1). *L.Ord.-U.Sil.*
      - Acanthograptidae (5). *?U.Cam., L.Ord.-M.Dev.*
    - Tuboidea *(order)* (12). *?U.Cam., L.Ord.-Sil.*
      - Tubidendridae (2). *L.Ord.(Tremadoc)-Sil.*
      - Idiotubidae (10). *?U.Cam.*(USSR), *L.Ord.-Sil.*
    - Camaroidea *(order)* (5). *Ord.*
      - Bithecocamaridae (1). *L.Ord.*

Cysticamaridae (4). *L.Ord.*
Crustoidea *(order)* (7). *L.Ord.-U.Ord.*
Wimanicrustidae (6). *L.Ord.-U.Ord.*
Hormograptidae (1). *U.Ord.*
Stolonoidea *(order)* (2). *Ord.*
Stolonodendridae (2). *Ord.*
Taxonomic Position Uncertain (24). *M.Cam.-Dev.*
Graptoloidea *(order)* (108;4). *L.Ord.(Arenig)-L.Dev.(?Emsian).*
Didymograptina *(suborder)* (54). *Ord.*
Dichograptidae (36). *L.Ord.*
Multiramous forms (21). *L.Ord.*
Goniograpti (13). *L.Ord.*
Temnograpti (2). *L.Ord.*
Schizograpti (5). *L.Ord.*
Dichograpti (1). *L.Ord.*
Pauciramous forms (15). *L.Ord.-U.Ord.*
Tetragrapti (3). *L.Ord.*
Didymograpti (12). *L.Ord.-U.Ord.*
Sinograptidae (6). *L.Ord.(U.Arenig-L.Llanvirn).*
Abrograptidae (3). *Ord.(?U.Arenig-Nemagraptus gracilis Z.)*
Corynoididae (2). *U.Ord.*
Nemagraptidae (5). *?L.Ord., U.Ord.*
Dicranograptidae (2). *L.Ord.-U.Ord.*
Glossograptina *(suborder)* (5). *Ord.*
Glossograptidae (4). *Ord.*
Cryptograptidae (1). *L.Ord.-U.Ord.*
Diplograptina *(suborder)* (35;3). *L.Ord.-U.Sil.*
Diplograptidae (9;3). *L.Ord.-L.Sil.*
Lasiograptidae (5). *Ord.*
Dicaulograptidae (1). *L.Ord.*
Peiragraptidae (1). *U.Ord.*
Retiolitidae (16). *U.Ord.-U.Sil.*
Retiolitinae (5). *U.Ord.-M.Sil.*
Archiretiolitinae (6). *U.Ord.*
Plectograptinae (5). *?L.Sil., M.Sil.-U.Sil.*
Dimorphograptidae (3). *L.Sil.*
Monograptina *(suborder)* (14;1). *L.Sil.-L.Dev.*
Monograptidae (6;1). *L.Sil.-L.Dev.*
Cyrtograptidae (8). *L.Sil.-L.Dev.*
Cyrtograptinae (3). *M.Sil.(Wenlock).*
Linograptinae (5). *L.Sil.-L.Dev.*
Graptolithina Incertae Sedis (4). *Ord.*
Group Graptoblasti (2). *L.Ord.(Tremadoc-Llandeilo).*
Group Acanthastida (1). *L.Ord.(Tremadoc).*
Group Graptovermida (1). *L.Ord.(Tremadoc).*
Unrecognizable genera (38).

## MORPHOLOGICAL TERMS APPLIED TO GRAPTOLITHINA AND OTHER HEMICHORDATA

Description of the morphology of various-rank divisions of the Hemichordata recognized in this book is given in several places under appropriate headings. Accordingly, it has seemed very desirable to organize a single alphabetically arranged glossary of morphological terms containing concise definitions and indicating typographically the relative importance attached to the different terms. Thus, most commonly used terms are printed in boldface capital letters (as **AUTOTHECA**), useful but less important terms in boldface small letters (as **clathria**), and least important (in part obsolete) terms in italic letters (as *solid axis*).

### *Glossary of Morphological Terms*

**adapertural plate.** Portion of apertural lobe in cucullograptids fused to ventral or dorsal wall of theca.

**amplexograptid theca.** Strongly geniculate theca with deep and long, rounded apertural excavations, generally with infragenicular selvage and typically with low rounded apertural lappets.

**anastomosis.** Temporary fusion, as of adjacent branches to form an ovoid mesh.

**ancora (ancora stage).** Anchor-shaped initial growth stage of retiolitids, apparently formed of virgella with two distal bifurcations.

**angular fuselli.** Extremely thin growth-bands of fusellar tissue filling angle between apertural margin and wall of succeeding theca (*see* Fig. 93,*5a*).

**annulus** (*pl.*, **annuli**). Internal ring on sicula and (rarely) early thecae of some monograptids, composed of fine irregularly laminated tissue.

**apertural spine.** Projection originating on margin of aperture; commonly single, less commonly paired.

**appendix.** Reticulate tubular structure at distal end of rhabdosome in Plectograptinae.

**aseptate.** Biserial rhabdosome lacking median septum.

**auriculate.** Expanded, earlike lateral lobes in highly modified thecae; e.g., cucullograptids, Crustoidea.

**AUTOTHECA.** Larger type of regularly-developed graptolite thecae, possibly containing female zooid (e.g., in Dendroidea) or hermaphrodite zooid (in Graptoloidea). (*See* also stolotheca.)

**axil.** Base of V-shaped bifurcation of dichotomously branched rhabdosomes, and especially bifurcation of dicranograptids.

**axonolipous.** Graptoloid rhabdosomes which are not scandent and therefore do not enclose nema.

**axonophorous.** Scandent biserial and uniserial graptoloids in which nema (virgula) is enclosed within rhabdosome or embedded in dorsal wall.

**basal disc.** Discoidal plate developed from apex of sicula for attachment of sessile graptolites, as in Dendroidea.

**biform.** Graptoloid rhabdosome (especially monograptids) with proximal and distal thecae of conspicuously different form.

**bilateral.** Graptoloid rhabdosome disposed more or less symmetrically to right and left of sicula.

**bipolar.** Bilateral monograptid rhabdosome with sicular cladium or pseudocladium.

**BISERIAL.** Scandent graptoloid rhabdosome with two series of thecae enclosing nema (virgula). (*See* also dipleural, monopleural.)

**BITHECA.** Smaller type of regularly-developed graptolite thecae, absent in Graptoloidea, possibly containing male zooid.

**branch.** *See* stipe.

**branching, dichotomous.** Division of stipe in which two branches diverge symmetrically from parent stipe.

**branching, lateral.** Division of stipe in which branch diverges at angle to parent stipe, which continues its original direction of growth.

*budding individual.* Term formerly used for stolotheca (now obsolete).

**camara.** Inflated proximal portion of autotheca in Camaroidea.

**central disc.** Web of sclerotized tissue uniting proximal ends of stipes in certain horizontal graptoloid rhabdosomes.

**cladium.** Rhabdosome developed from sicular or thecal aperture in Cyrtograptidae. (*See* also metacladium, procladium, pseudocladium.)

**clathria.** Skeletal framework of rods (lists) composing rhabdosome, in some supporting reticulum or attenuated periderm.

**climacograptid theca.** Strongly geniculate theca with straight or slightly convex supragenicular wall parallel to axis of rhabdosome and relatively short (narrow) apertural excavation.

**COENOECIUM.** Tubular exoskeleton of colonies or associations of Pterobranchia.

**collum.** Erect tubular (distal) portion of autotheca in Camaroidea.

**colony.** *See* rhabdosome.

*common canal.* Term sometimes used for continuous tubular cavity collectively formed by prothecae of graptoloid; rarely involving some portion of metathecae.

**complete septum.** *See* median septum.

**CONOTHECA.** Relatively large, conical theca with small circular aperture, irregularly developed on rhabdosomes of certain Tuboidea.

**corona (corona stage).** Inflated reticulate proximal end of retiolitids succeeding ancora stage in development.

**CORTICAL TISSUE.** Outer layer of finely, rather irregularly laminated tissue composing graptolite periderm *(q.v.)*.

**CROSSING CANAL.** Proximal (prothecal) portion of graptoloid theca which grows across axis of sicula to develop on side opposite that of its origin.

**cryptoseptate.** Biserial rhabdosomes in which median septum is composed of peridermal rods arranged as in septate forms, but lacking peridermal septal membrane.

**cysts.** Vesicles of varying size and shape occurring in autothecal cavities of Crustoidea.

**declined.** Graptoloid rhabdosome with branches hanging below the sicula, subtending an angle less than 180° between their ventral sides (*see* Fig. 38).

**deflexed.** Similar to declined but with distal extremities of stipes tending to horizontal (*see* Fig. 38).

**dendroid** (habit of growth). Bushy colony formed by irregular branching.

**denticulate.** Sharply pointed thecal apertures provided with short spine or mucro.

**diad budding.** Mode of budding in Tuboidea resulting in two zooids at each nodal division, lacking regularity of thecal succession.

**DICALYCAL THECA.** Graptoloid theca giving rise to two buds (c.f. normal asexual reproduction in which single bud is produced by each zooid).

**dicellograptid theca.** Geniculate theca characterized by introversion, usually accompanied by some degree of isolation of apertural region.

**dichograptid theca.** Straight, almost parallel-sided tubular theca.

**dichotomous.** *See* branching.

**DIPLEURAL.** Biserial graptoloid rhabdosome in which two stipes are in back-to-back contact so that each stipe has two external walls.

**dissepiment.** Strand of cortical periderm serving to connect adjacent branches in dendroid rhabdosome (especially *Dictyonema*).

**DISTAL.** Last-formed part (of stipe, theca, etc.) farthest away from point of origin.

**DORSAL.** Side of stipe opposite thecal apertures, or comparable side of thecal aperture; not necessarily related to position of growth, but presumably related to dorsal side of zooid.

**everted.** Plane of aperture facing outward (cf. introverted, retroverted); may be associated with angular fuselli *(q.v.)*.

**extensiform.** Didymograptid with horizontal stipes.

**flabellate** (habit of growth). Rhabdosome fan-shaped, with stipes spread out in single plane.

**FUSELLAR TISSUE.** Inner layer of periderm, generally composed of alternating L and R growth bands or fuselli.

**genicular spine.** Sharp projection originating on geniculum; commonly single, rarely paired.

**GENICULUM.** Angular bend in direction of growth of graptoloid theca, especially climacograptid or lasiograptid; hence supragenicular, infragenicular.

**glyptograptid theca.** Sinuous theca with smooth curve in place of angular geniculum and convex supragenicular wall.

*gonangium.* Term formerly used for bitheca (now obsolete).

**gymnocaulus.** Unsclerotized stolon situated behind terminal bud in *Rhabdopleura,* from which zooids are proliferated.

**gymnograptid theca.** Sharply geniculate theca with extremely short supragenicular wall directed inward distally and generally with deep and long, rounded apertural excavation.

**horizontal.** Graptoloid rhabdosome with stipes disposed in plane at right angles to axis of sicula.

*hydrosome.* Obsolete term for rhabdosome.

*hydrotheca.* Obsolete term for autotheca of dendroids and other groups and for theca of graptoloids.

**incomplete septum.** *See* median septum.

**INITIAL BUD.** Outgrowth through foramen in sicular wall producing first theca of rhabdosome; stolotheca of dendroids, etc., prothecal portion of first theca of graptoloids.

**interthecal septum.** Peridermal membrane separating overlapping thecal cavities in Graptoloidea, comprising dorsal wall of one theca and part of ventral wall of succeeding theca.

**introverted.** Plane of aperture facing inward (dorsally), resulting from excessive growth of ventral wall of theca usually accompanied by sigmoidal curvature of thecal axis.

**isolation.** Separation of distal (metathecal) portions of thecae from stipe, as in *Rastrites,* or distal portions of autothecae of Dendroidea, etc.

**lacinia.** Delicate skeletal network, extraneous to rhabdosome proper, supported on spines.

**lacuna stage.** Final period in development of porus in monograptids, where notch or sinus is closed by fusellar growth bands.

**languette.** Laterally expanded ventral apertural process of theca.

**lappet.** Broad, rounded, lateral apertural process of theca (or sicula).

**lasiograptid theca.** Sharply geniculate theca with supragenicular wall directed inwards distally and deep, moderately long, rounded apertural excavation; less extreme than gymnograptid.

**leptograptid theca.** Theca with rounded geniculum and very long supragenicular wall typically parallel to axis of stipe.

**list.** Skeletal rod strengthening periderm in Graptoloidea, a unit of clathria.

**lophophore.** Paired arms or groups of arms, ciliated and bearing tentacles, situated adjacent to mouth of zooid; functionally food-collecting and respiratory.

**MEDIAN SEPTUM.** Partition in biserial graptoloids separating two series of thecae. Its relationships in monopleural rhabdosomes are imperfectly known. In dipleural forms it appears to be a single membrane and arises between daughter thecae of dicalycal theca; thus a complete septum arises between the 4th $(th2^2)$ and 5th $(th3^1)$ thecae, an incomplete septum arises between some later pair, and a partial septum occurs on one side only, thecae appearing to alternate on opposite sides.

**mesial.** Middle portion of free ventral wall (supragenicular wall) of theca; hence mesial spine.

**metacladium.** Term proposed for thecal or sicular cladium as opposed to procladium or main stipe.

**METASICULA.** Distal portion of sicula composed of normal fusellar growth bands. (*See* also prosicula.)

**METATHECA.** Distal portion of graptoloid theca, morphologically equivalent to autotheca of dendroids, etc. (*see* also protheca).

**microfusellar tissue.** Fusellar substance composed of extremely fine and somewhat irregular growth bands; genicular flanges are generally composed of microfusellar tissue.

**microtheca.** Type of autotheca occurring in Tuboidea, with narrow terminal portion and differently oriented apertures.

**monofusellar tissue.** Type of fusellar substance laid down in single, not alternating, series of growth bands.

**MONOPLEURAL.** Biserial graptoloid rhabdosome in which two stipes are in contact laterally (Glossograptina) so that each stipe has only one external wall (*see* Fig. 62).

**monopodial growth.** Type of colonial growth with permanent terminal zooid behind which new zooids arise as stem elongates. (Cf. sympodial.)

**multiramous.** Branches numerous.

**NEMA** (*pl.,* **NEMATA**). Threadlike extension of apex of prosicula, extending embryonic *nema prosiculae;* probably solid in adult rhabdosomes. May have served for attachment or may terminate in disc of attachment or vanelike "float" structures.

**OBVERSE.** Aspect of graptoloid rhabdosome (especially early growth stages or biserial forms) in which sicula is most completely visible. (Cf. reverse).

**occlusion.** Sealing of thecal aperture by sclerotized film.

**orders** (of branching). Successive divisions of dichotomous branches, or successive generations of cladia.

**orthograptid theca.** Straight, parallel-sided, tubular theca of biserial graptoloid.

**partial septum.** *See* median septum.

**pauciramous.** Branches comparatively few.

**pectocaulus.** Sclerotized stolon (or "black stolon") embedded in lower surface of mature parts of coenoecium of *Rhabdopleura.*

**pendent.** With approximately parallel branches hanging below sicula (*see* Fig. 38).

**pericalycal.** Mode of development of scandent (monopleural) rhabdosomes associated with dicalycal $th1^1$ and left-handed origin of $th1^2$, sicula becoming largely enclosed on both sides during subsequent development. (Cf. platycalycal.)

**PERIDERM.** Horny substance of scleroproteic composition forming skeleton of Graptolithina, comprising inner (fusellar) layer with growth bands and growth lines and outer (cortical) layer of finely laminated tissue.

**platycalycal.** Mode of development, especially of scandent dipleural rhabdosomes, associated with dicalycal $th2^1$ and concentration of budding on reverse side. (Cf. pericalycal.)

**polymorphic.** Colony comprising more than one kind of zooid, or rhabdosome with more than one type of theca.

**porus.** Circular opening in wall of sicula through which initial bud passes to exterior; generally produced by resorption, but in monograptids arises as apertural notch (sinus) during growth of sicula.

**preoral lobe.** Anterior glandular lobe or disc in pterobranchs, which secretes coenoecium.

**procladium.** Term proposed for main stipe of cladia-bearing rhabdosome, normal cladia then being distinguished as metacladia.

**PROSICULA.** Proximal, initially formed part of sicula, apparently secreted as single conical unit with faintly marked spiral thread; at later stage longitudinal fibers are added.

**prosoblastic.** Type of diplograptid development in which $th2^1$ and ultimately $th1^2$ grow upward (distally) from their origin. (Cf. streptoblastic.)

**PROTHECA.** Proximal portion of graptoloid theca before differentiation of succeeding theca; morphological equivalent of stolotheca of dendroids and other groups.

**prothecal fold.** Inverted U-shaped curvature of part of protheca (usually initial portion) giving noded appearance to dorsal margin of stipe in certain axonolipous graptoloids, or similarly placed swellings (rare) in monograptids.

**PROXIMAL.** First-formed portion (of rhabdosome, stipe, theca, etc.) nearest point of origin.

**pseudocladium.** Term proposed for regenerated portion of bipolar rhabdosome lacking sicula.

**pseudovirgula.** Virgula of thecal or sicular cladium, originating as thecal or sicular apertural spine.

**quadriserial.** Scandent graptoloid rhabdosome composed of four rows of thecae in "back-to-back" contact *(Phyllograptus)*.

**reclined.** Graptoloid rhabdosome with branches growing upward, subtending an angle less than 180° between their dorsal sides (*see* Fig. 38).

**reflexed.** Similar to reclined, but with distal extremities of the stipes tending to horizontal (*see* Fig. 38).

**reticulum.** Delicate irregular network, usually supported on clathria, replacing continuous periderm in retiolitids.

**retroverted.** Thecal apertures facing proximally in consequence of hooked or reflexed shape of metatheca, following excessive growth of dorsal wall of theca.

**REVERSE.** Aspect of graptoloid rhabdosome (especially early growth stages or biserial forms) in which sicula is more or less concealed by crossing canal(s).

**RHABDOSOME.** Sclerotized exoskeleton of entire graptolithine colony; includes compound rhabdosomes with cladia, but not associations of rhabdosomes. (*See* synrhabdosome.)

**root.** Irregular branching structure (cortical tissue) developed from apex of sicula serving for attachment of sessile dendroids, etc.

**scalariform.** Preservational view presenting ventral (thecal) aspect of graptoloid rhabdosome, especially biserial forms.

**SCANDENT.** Graptoloid rhabdosome with stipes growing erect (distally), enclosing or including nema (virgula) (*see* Fig. 38).

**sclerotized.** Hardening due to secretion of scleroproteic substances by zooid(s). (It is now known that chitin is completely lacking in graptolite periderm.)

*scopulae.* Peculiar ramifying fibrous development from edges of median septum (as in lasiograptids) comparable with lacinia.

**selvage.** Thickened margin, especially of aperture.

**septal.** Related to septum.

**septum.** *See* interthecal septum, median septum.

**SICULA.** Skeleton of initial zooid of colony, comprising conical prosicula and tubular distal metasicula.

**sinus stage.** Initial phase in development of porus in monograptids, consisting of notch in apertural margin.

*solid axis.* Obsolete term for virgula of graptoloids.

**STIPE.** One branch of branched rhabdosome or entire colony of unbranched rhabdosome.

**stolon.** Thin sclerotized sheath presumably surrounding unsclerotized thread of soft tissue, from which thecae appear to originate in Dendroidea and other groups; comparable to pectocaulus of pterobranchs.

**STOLOTHECA.** One of three principal types of theca (cf. autotheca and bitheca) enclosing main stolon and proximal portions of daughter stolotheca, autotheca and bitheca; probably secreted by immature autozooid and constituting in effect proximal portion of autotheca; equivalent to protheca of graptoloid.

**streptoblastic.** Type of diplograptid development in which significant portion of proximal parts of $th1^2$, $th2^1$ and even $th2^2$, grow downward. (Cf. prosoblastic.)

**sympodial growth.** Type of colonial growth in which each zooid is in turn terminal zooid of its branch. (Cf. monopodial.)

**synrhabdosome.** Association of several (usually biserial) graptoloids attached distally by their nemata to common center.

**THECA.** Sclerotized tube or cup enclosing any zooid of rhabdosome (other than sicula); term generally used to denote autotheca of Graptoloidea, which are not polymorphic.

**thecal grouping.** More or less regular association of groups of autothecae and bithecae forming small branches (twigs), particularly in acanthograptids.

**thecorhiza.** Encrusting basal disc in Tuboidea, composed principally of stolothecae, from which autothecae and bithecae arise singly, in clusters, or as branches.

**triad budding.** Mode of budding in Dendroidea and Crustoidea in which three zooids are produced at each division, with regular succession of thecae. *See* Wiman rule.

**triangulate theca.** Type of isolate monograptid theca, triangular in lateral view, with retroflexed aperture.

**twig.** *See* thecal grouping.

**umbellate theca.** Type of autotheca in some Tuboidea, characterized by enlarged, reflexed, umbrella-shaped hood extending back over aperture of preceding autotheca (*see* Fig. 25).

**UNISERIAL.** Rhabdosome or stipe of graptoloid consisting of single row of thecae only. (Cf. biserial, quadriserial.)

**VENTRAL.** Side of stipe on which thecal apertures are situated or comparable side of thecal aperture; not necessarily related to position of growth of rhabdosome, but assumed to be related to ventral side of zooid.

**vesicular diaphragm.** Globular swelling on main stolon at nodes or points of origin of daughter stolons.

**VIRGELLA.** Spine developed during growth of metasicula, embedded in sicular wall and projecting freely from its apertural margin.

**virgellarium.** Umbrella-shaped structure developed at tip of virgella in linograptids.

**virgula.** Term commonly used for nema of scandent graptoloids.

**Wiman rule.** Process of budding resulting in regularly alternating triads of autotheca, bitheca, and stolotheca, diagnostic of Dendroidea.

**ZOOID.** Soft-bodied individual inhabiting theca or coenoecial tube (e.g., thecal zooid, siculozooid).

## STRATIGRAPHICAL NOTE

Following current practice in the *Treatise,* the Tremadoc Series is classed as the lowermost division of the Ordovician, not, as in most British works, as uppermost Cambrian. A good deal of confusion relates to the Lower-Middle and the Middle-Upper Ordovician boundaries in various parts of the world. I follow here the solution accepted by WHITTINGTON & WILLIAMS (1964) of recognizing only two divisions, Lower and Upper, drawing the boundary at the base of the *Nemagraptus gracilis* Zone. This species is widely distributed and constitutes a horizon that can be recognized confidently in most graptolite sequences. The Silurian is divided into the conventional Lower, Middle, and Upper (Llandovery, Wenlock, and Ludlow of the British succession), but it should be noted that the last is extended up to the base of the *Monograptus uniformis* Zone, which is currently accepted as the boundary between the Silurian and Devonian systems.

# HEMICHORDATA

## Phylum HEMICHORDATA Bateson, 1885, emend. Fowler, 1892

[*nom. transl.* HYMAN, 1959, p. 74 (*ex* class Hemichordata BATESON, 1885, p. 111)] [=Stomochorda DAWYDOFF, 1948, p. 367 (subphylum)]

For reasons discussed in the section on "General Features" (p. *V*5), it is not possible to give a collective diagnosis covering living and extinct classes here assigned to the Hemichordata. Where the organism is known, it exhibits the essential embryological features of the Deuterostomia and also possesses pharyngeal openings (except in *Rhabdopleura*), but it lacks the endostyle and notochord distinctive of the phylum Chordata. When present, the coenoecium or rhabdosome consists of fusellar tissue, with or without an external laminated cortical tissue, and the substance of this is scleroproteic in composition.

The Hemichordata comprise the two extant classes, Enteropneusta and Pterobranchia. The former are unknown fossil, but the pterobranchs are known as exceedingly rare fossils dating back to the Tremadoc, their representatives thus being contemporary with the graptolites. The extremely rare living organism *Planctosphaera* is generally assigned to a separate (third) class, and for taxonomic convenience the Graptolithina are accepted here as a fourth and extinct class of the phylum. *M.Cam.-Rec.*

# ENTEROPNEUSTA

## Class ENTEROPNEUSTA
## Gegenbaur, 1870

[*nom. correct.* HAECKEL, 1879 (*pro* Enteropneusti GEGENBAUR, 1870, p. 158)] [=Hemichordata BATESON, 1885]

Free, with elongate wormlike body and pronounced division into an acorn-shaped proboscis (protosoma), collar (mesosoma), and trunk (metasoma); branchial apparatus well developed as a long double row of pores strengthened by a cuticular branchial skeleton. *Rec.*

The class is unknown fossil;[1] among numerous living genera, the following may be mentioned:

**Balanoglossus** DELLE CHIAJE, 1829, p. 141 [**B. clavigerus;* M]. Widely distributed around Atlantic and Pacific coasts.

**Ptychodera** ESCHSCHOLTZ, 1825. p. 740 [**P. flava;* M]. IndoPac.-W.Indies.

**Saccoglossus** SCHIMKEWITSCH, 1892, p. 93 [**Balanoglossus mereschkowskii* WAGNER, 1885, p. 46; M]. N.Atl.-White Sea-Japan-N.Z.——FIG. 1. *S. pusillus* RITTER, White Sea; ×0.7 (48).

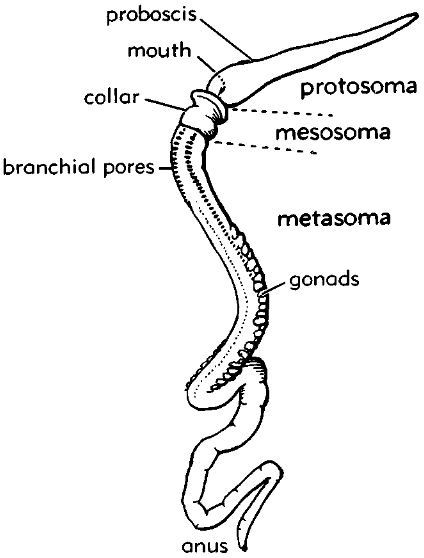

FIG. 1. A typical enteropneustan, *Saccoglossus pusillus,* showing the principal external features of the body (48).

# PTEROBRANCHIA

## Class PTEROBRANCHIA
## Lankester, 1877

[Class Pterobranchia LANKESTER, 1877, p. 448]

Fixed colonial or pseudocolonial organisms; body compact and without conspicuous division into three parts; middle segment (mesosoma) small but with one or more pairs of arms furnished with ciliated tentacles (=lophophore); posterior segment (metasoma) with long stalk or peduncle by which the zooid may be attached; branchial apparatus rudimentary; cuticular skeleton external. *L.Ord.(Tremadoc)-Rec.*

## MORPHOLOGY

The body of pterobranchiates is small (2 to 7 mm. in *Cephalodiscus*) or even microscopic (less than 0.5 mm. in *Rhabdopleura*), and its most conspicuous feature is the **lophophore** structure developed from the mesosomal or collar segment, which gives it a pronounced bilateral symmetry and a superficially polyzoan appearance (Fig. 2,*1*). The lophophore consists of one pair of arms in *Rhabdopleura,* and many pairs in *Cephalodiscus,* and contains an extension of the collar coelom into the arms and tentacles. The preoral lobe (protosoma) forms a glandular cephalic disc which posteriorly overhangs the mouth. Only in embryonic stages is the mesosomal segment clearly differentiated from the trunk segment, and from the ventral side of the sac-like trunk arises the **peduncle** or contractile stalk. In *Rhabdopleura* this is of considerable length and serves to attach the organism at the base of its tube to the

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[1] What appears to be a giant abyssal enteropneust was photographed at the end of a "spiral" fecal cast at a deep-water Pacific station, as described by BOURNE & HEEZEN (*Science,* v. 150, 1965, p. 60), and the form of this cast is reminiscent of some trace fossils such as *Taphrhelminthopsis* that have been described from Alpine flysch. Comparable tracks are known, however, to be made by other types of organism. Burrows attributed to Enteropneusta have been described from the Muschelkalk of the Holy Cross Mountains by KAŹMIERCZAK & PSZCZÓŁKOWSKI (1969) with references to previous records from German Trias by SOERGEL (1923) and MAGDEFRAU (1932).

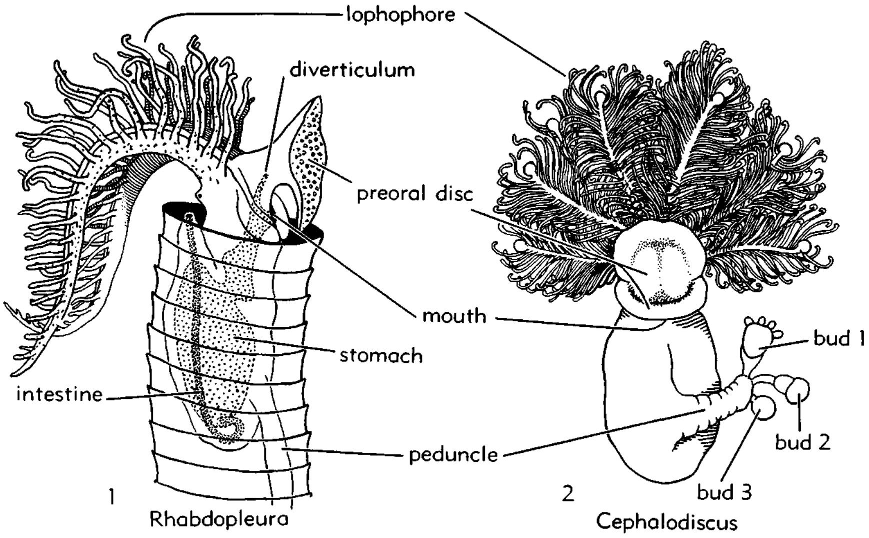

FIG. 2. Enlarged drawings of *(1) Rhabdopleura* and *(2) Cephalodiscus* showing the principal external features of the body in the Pterobranchia (48).

**pectocaulus** or stolon; it is shorter in *Cephalodiscus* and free, the organisms living not in true colonies but in associations.

The mouth opens into a large pharyngeal region, from the roof of which is given off anteriorly a small diverticulum formerly regarded as the homologue of the notochord. Laterally the pharynx is developed into a branchial region with a single pair of branchial pores in *Cephalodiscus,* whereas in *Rhabdopleura* the whole branchial structure is rudimentary. Posteriorly, the pharynx leads into a capacious stomach, from which a straight intestine doubles back to the anal pore situated on a dorsal prominence in the front part of the trunk segment (Fig. 2). The gonads are paired in *Cephalodiscus,* single in *Rhabdopleura;* the sexes are separate except in certain species of *Cephalodiscus* where hermaphrodite individuals occur. Males and females usually are indistinguishable, but some species are dimorphic and in *C. sibogae* the males are degenerate. Asexual reproduction (budding) is common in both genera.

The blood system comprises few main vessels, centered on a cardiopericardial vesicle situated in the protosoma; this is claimed to be homologous with the madreporic vesicle of larval echinoderms. The nervous system is rudimentary, with a central ganglion near the base of the lophophore.

A cuticular exoskeleton is secreted both by *Cephalodiscus* and *Rhabdopleura.*

## Order RHABDOPLEURIDA Fowler, 1892

[Rhabdopleurida FOWLER, 1892, p. 297]

Truly colonial animals with zooids attached by a contractile stalk to the stolon or pectocaulus; zooids provided with one pair of arms; gonads unpaired; no branchial pores. The skeleton (coenoecium) consists of an irregularly branching system of sclerotized tubes, attached to the surface of a pebble or shell, from which slender free zooidal tubes rise erect. Creeping and zooidal tubes are alike composed of regular growth bands that are clearly defined by transverse growth lines, and the pectocaulus is embedded in the base of the creeping tube. *L.Ord.-Rec.*

Growth of the colony is by distal extension of the soft stolon (gymnocaulus) bearing at its extremity a permanent terminal bud ("blastozooid *inachevé*"). This terminal bud secretes the adnate or creeping tube as it advances. According to SCHEPOTIEFF, this tube is a closed, pointed tube; but

LANKESTER describes it as an open-ended tube. Normal zooidal buds develop successively behind the terminal bud on the gymnocaulus, forming a linear series with the youngest always nearest to the terminal bud (Fig. 3). As each develops, it becomes sealed off by a transverse partition across the creeping tube, and at about this stage the gymnocaulus becomes sclerotized to form the black stolon or pectocaulus (some 20 microns in diameter) and becomes embedded in the lower wall of the creeping tube. Each zooid in turn then forms by resorption a circular pore at the distal end of its chamber, and the zooid emerges, secreting as it grows upward the slender, erect, free portion of the zooidal tube. Branching occurs when one of the buds develops into a terminal bud instead of a normal zooid and starts to form its own creeping tube. Initial stages of development of the colony are only very imperfectly known.

Growth bands of the creeping tube are laid down in the form of half segments deposited alternately to left and right, so that the growth lines exhibit a characteristic median zigzag suture; the free zooidal tube consists of complete rings of periderm, each intersected by a single oblique suture marking the beginning and end of its formation. The initial rings at the base of the free zooidal tube are of course laid down discordantly on the growth bands of the creeping tube.

## Family RHABDOPLEURIDAE Harmer, 1905

[Rhabdopleuridae HARMER, 1905, p. 5]

Characters of the order. *L.Ord.-Rec.*

**Rhabdopleura** ALLMAN, 1869, p. 58 [**R. normani;*

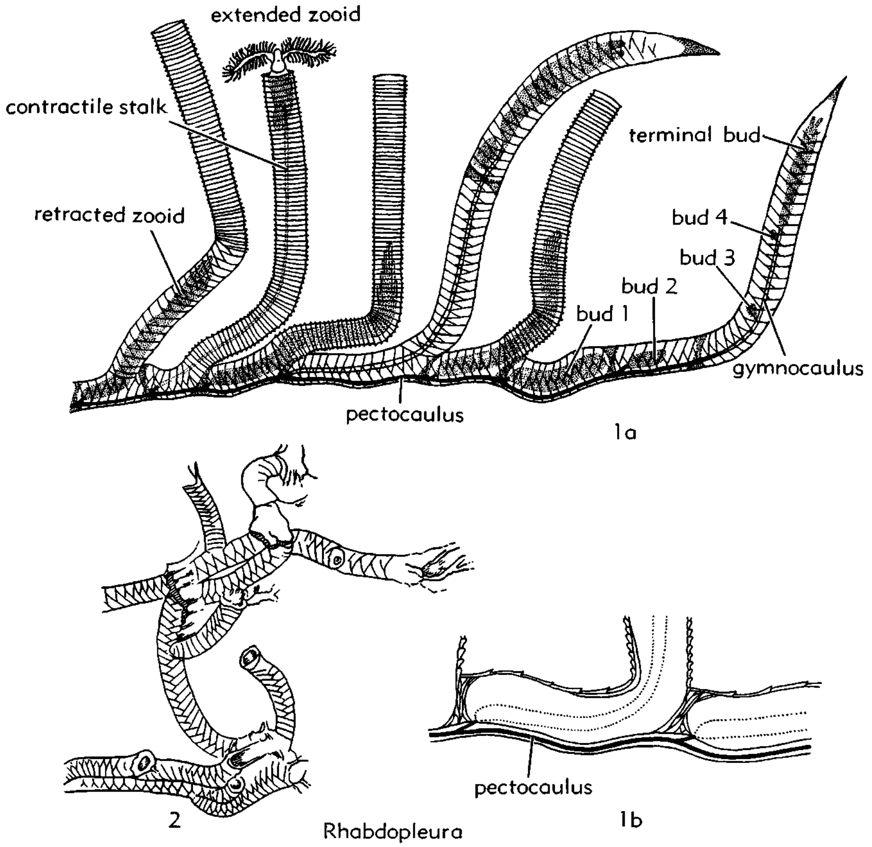

FIG. 3. Rhabdopleurida (Rhabdopleuridae) (p. V15).

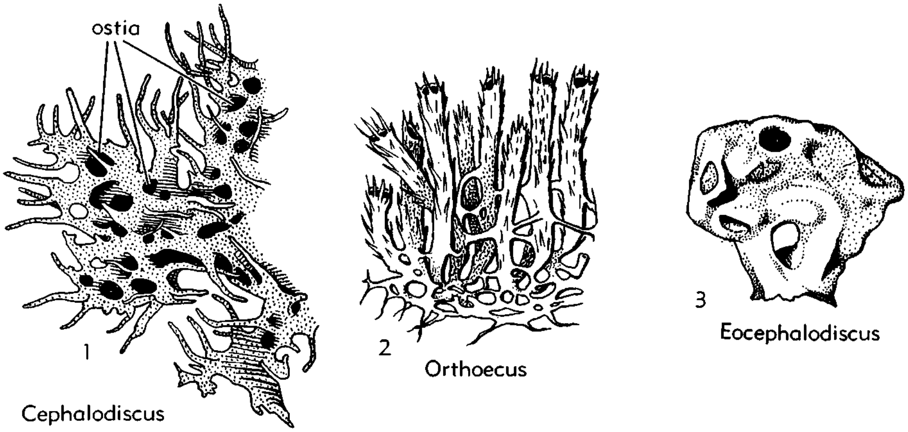

FIG. 4. Cephalodiscida (Cephalodiscidae) (p. *V*17).

M]. *U.Cret.*(Pol.)-*Eoc.*(Eng.)-*Rec.*(E.Atl.-S.Pac.-Antarctic).——FIG. 3,*1*. **R. normani,* Rec.; *1a,* portion of coenoecium of living specimen showing expanded and retracted zooids, developing buds, terminal bud, and characteristic growth lines of creeping and zooidal tubes, ×20 (114); *1b,* long sec. of part of coenoecium showing pectocaulus, transv. partitions, and relations of growth bands, ×25 (23).——FIG. 3,*2*. *R. eocenica* THOMAS & DAVIS, M.Eoc., S.Eng.; ×12 (235).

**Rhabdopleurites** KOZŁOWSKI, 1967, p. 126 [**R. primaevus,* p. 127; OD]. Similar to *Rhabdopleura. Ord.*(glacial boulder), Eu.(Pol.).

**Rhabdopleuroides** KOZŁOWSKI, 1961, p. 4 [**R. exspectatus;* M]. Coenoecial tubes attached throughout their length; aperture with languette. *L.Ord.* (glacial boulders), Eu.(Pol.).

## Order CEPHALODISCIDA Fowler, 1892

[Cephalodiscida FOWLER, 1892, p. 297]

Zooids forming free unattached associations, not true colonies; lophophore composed of several pairs of arms; gonads paired; one pair of branchial pores; coenoecium extremely variable and generally irregular in form. *L.Ord.(Tremadoc)-Rec.*

The coenoecium of cephalodiscids is extremely variable in form, encrusting, dendroid or compact, and it may be elaborately spined. In the majority of species, separate zooidal tubes are formed, usually connected by cuticular substance; or somewhat rarely, completely embedded in it; in a few forms, the superficial openings (ostia) lead into a general cavity occupied by all the zooids and their buds. Where distinct zooidal tubes are present, usually they do not communicate with one another, and buds produced from the peduncle or stalk free themselves from the parent before secreting their own tubes. Zooids are able to leave their tubes and creep about the coenoecium, and in this way to secrete the connective cuticular tissue. In the less compact types of coenoecium, the zooidal tubes are seen to be formed of growth bands comparable with those of *Rhabdopleura* but irregular in form and spacing.

### Family EOCEPHALODISCIDAE Kozłowski, 1949

[Eocephalodiscidae KOZŁOWSKI, 1949, p. 195]

Chambers relatively few (about 10), forming a compact, minute, unspined coenoecium. *L.Ord.(Tremadoc).*

**Eocephalodiscus** KOZŁOWSKI, 1949, p. 195 [*E. polonicus;* OD]. *L.Ord.(Tremadoc),* Pol.——FIG. 4,*3*. **E. polonicus;* ×20 (114).

### Family CEPHALODISCIDAE Harmer, 1905

[Cephalodiscidae HARMER, 1905, p. 5]

Coenoecium relatively large, variable in form, with or without individual zooidal tubes, or rarely absent altogether. *Ord., ?Tert., Rec.*

**Cephalodiscus** M'INTOSH, 1882, p. 348 [**C. dodecalophus;* M]. Several subgenera based on form of coenoecium. *Rec.,* S.Hemis.(almost exclusively). [Silicified tubes from *M.Eoc.,* France, provisionally referred to this genus.]

**C. (Cephalodiscus)** [=*Demiothecia* RIDEWOOD, 1906, p. 191]. Coenocium branching, each ostium leading into cavity which is occupied in common by all zooids and their buds. *Rec.,* Antarctic.——FIG. 4,*1*. *C. (C.) hodgsoni* (RIDEWOOD); approx. ×1.5 (48).

**C. (Idiothecia)** LANKESTER in RIDEWOOD, 1906, p. 191 [**Cephalodiscus nigrescens* LANKESTER, 1905, p. 400; SD BULMAN, herein]. Coenoecium branching, composed of individual zooidal tubes embedded in common coenoecial substance. *Rec.,* Antarctic.

**C. (Orthoecus)** ANDERSSON, 1907, p. 11 [**Cephalodiscus solidus,* p. 11; SD BULMAN, herein]. Zooids with individual tubes embedded in common coenoecial substance to form irregular mass. *Rec.,* Pac.(E.Indies).——FIG. 4,*2*. *C. (O.)* sp.; approx. ×1.5 (48).

**C. (Acoelothecia)** JOHN, 1931, p. 259 [**C. (A.) kempi;* M]. Colony in form of branched network of spines and bars without definite coenoecial cavities. *Rec.,* Antarctic (Falkland Is.).

**Atubaria** SATO, 1936, p. 105 [**A. heterolopha;* M]. Without any coenoecium. *Rec.,* Pac.(Japan).

**Pterobranchites** KOZŁOWSKI, 1967, p. 123 [**P. antiquus;* OD]. Coenoecium of irregularly aggregated tubes and elongated vesicles. *L.Ord.*(glacial boulder), Eu.(Pol.).

# PLANCTOSPHAEROIDEA

## Class PLANCTOSPHAEROIDEA van der Horst, 1936

[Planctosphaeroidea VAN DER HORST, 1936, p. 612]

This class is based on two specimens from the Bay of Biscay believed to represent the larval form of an unknown type of Hemichordata. *Rec.*

# GRAPTOLITHINA

## DIAGNOSIS AND GENERAL FEATURES

### Class GRAPTOLITHINA Bronn, 1846

[Graptolithina BRONN, 1846, p. 149 (*nom. transl.* ELLES, 1922, p. 168)]

The Graptolithina are colonial, marine organisms which secreted a sclerotized exoskeleton with characteristic growth bands (fuselli) and growth lines. The thecae housing individual zooids are usually arranged in a single or double row along the branches (stipes) of the colony (rhabdosome), rarely in irregular aggregates. In most orders, the thecae are polymorphic and in three they are clearly related to an internal sclerotized stolon system. Rhabdosomes originate by a single bud from the initial zooid, housed in a conical sicula, producing simple, branched or rarely encrusting colonies. Sessile or pelagic. *M. Cam.-Carb.*

Six orders are now recognized: 1) Dendroidea NICHOLSON, 1872; 2) Tuboidea KOZŁOWSKI, 1938; 3) Camaroidea KOZŁOWSKI, 1938; 4) Crustoidea KOZŁOWSKI, 1962; 5) Stolonoidea KOZŁOWSKI, 1938; 6) Graptoloidea LAPWORTH, in HOPKINSON & LAPWORTH, 1875.

These are based principally on details of branch structure, which in turn reflects the nature and regularity of stolonal budding. An additional order, Dithecoidea, has been proposed by OBUT (1964), but since its branch structure has not been conclusively demonstrated, the genera concerned are here grouped together with others of uncertain taxonomic position under the general heading "Taxonomic Position Uncertain" (p. *V*54). Other groups of unknown affinity are the Graptovermida, Graptoblasti, and Acanthastida (p. *V*136-*V*139).

## PIONEER WORK ON GRAPTOLITES

In the early days of paleontology, graptolites attracted comparatively little attention. Their remains were thought originally to be those of plants although LINNÉ believed them to be inorganic when bestowing the name *Graptolithus* upon *G. sagittarius* and *G. scalaris,* and it appears that WAHLENBERG (1821) was the first to recognize their animal nature. The generic name *Graptolithus* now has been suppressed by the International Commission on Zoological Nomenclature (Opinion 197), but it persists in the forms Graptolithina, Graptoloidea, and the anglicized version "graptolites."

The early phase of work by BRONN (1834), BECK (1839), and others, followed towards the middle of the century by publications of M'COY, BARRANDE, and SALTER, has given us a number of well-known generic names; but probably the first work of real insight and understanding is HALL's *Graptolites of the Quebec Group* (1865), where more than a dozen genera and over 50 species of graptolites (including dendroids) were described and beautifully figured.

Soon after this began the period of LAPWORTH's great contribution with a series of papers (extending mainly from 1870 to 1880) devoted not only to a more exact understanding of structure and morphology and a more precise determination of species, but above all to the demonstration of their stratigraphical value (see especially his *Geological Distribution of the Rhabdophora,* 1879-80). This phase of work on the group may be said to have culminated in the *Monograph of British Graptolites* (1901-18) where LAPWORTH was assisted by Miss ELLES and Miss WOOD to produce an exhaustive and superbly illustrated monograph which has been an indispensable aid to workers all over the world. Comparable work was being done in Sweden, at first by LINNARSSON (who published but little), later by TÖRNQUIST and HADDING, while RUEDEMANN's *Graptolites of New York* (1904-08) and his *Graptolites of North America* (1947) serve the same need for the North American continent.

Toward the end of last century a remarkable series of papers was published by HOLM (1890, 1895) and WIMAN (1895-1901), who may be said to have initiated the really detailed study of graptolite morphology, aided by novel techniques of solution and serial sectioning. After an interval of nearly 30 years, a revival of interest in the application of special techniques began with KRAFT's (1926) memoir on *Diplograptus* and *Monograptus,* and much of HOLM's work which was left unpublished at his death was completed in a series of papers by BULMAN (1932-36). The outstanding contribution of this character, however, was that of KOZŁOWSKI (1938, 1949), whose researches on the astonishingly well-preserved material from silicified nodules in Tremadocian rocks of Poland led to a new concept of the nature and affinities of the Graptolithina. Since then a steadily increasing emphasis (especially in Britain, Poland and Scandinavia) has been placed on detailed morphological description and analyses.

## TECHNIQUES

### PREPARATION OF SPECIMENS

Detailed information about structure and development of graptolites is obtained almost entirely from specimens which have been dissolved out of their matrix and rendered more or less transparent by the use of various oxidizing agents. The actual processes and reagents employed naturally depend upon the nature of the matrix and the degree of carbonization of the fossil.

Pure limestone matrix can be dissolved readily with hydrochloric or acetic acid, the latter being sometimes preferable with fragile material on account of its more gentle action. The concentration should be adjusted so that effervescence is not too brisk, and is maintained by repeated addition of drops of concentrated acid. The condition of preservation of the graptolite periderm is an important factor, and some limestone material otherwise suitable is rendered useless for treatment because the graptolite remains have been too highly carbonized and have become so brittle that they crumble to a powder when freed from matrix.

Impure limestone generally requires a double treatment, involving solution of the calcareous matter first and then (after washing out all trace of HCl) solution or disintegration of the arenaceous or argillaceous remainder with hydrofluoric acid. Repeated washing and decanting is necessary to remove all HF before the graptolite remains can be picked out with a pipette under low-power binocular. Much of the fine mud can be removed by elutriation, and some workers wash the whole through a series of sieves, although a greater risk of breakage is entailed in this process. Graptolites preserved in chert nodules of course can be dissolved out with HF without previous treatment.

Graptolites which have been dissolved out of calcareous rocks may contain bubbles of $CO_2$ which should be removed in a vacuum desiccator before further treatment. Clearing is most usually done in a watch-glass with potassium chlorate and concentrated nitric acid, but *eau de Javelle* and other bleaching reagents have been used. The period required varies with the thickness of periderm and the degree of carbonization, and can only be judged individually by constant observation through a low-power binocular; but the treatment cannot be prolonged, as a rule, beyond 20 minutes or half an hour without the specimens becoming too brittle to handle. Some workers prefer a much lower concentration over a correspondingly greater period of time. Quite a high proportion of material successfully dissolved from its matrix proves unsuitable for further treatment of this kind.

Specimens which cannot be cleared are best mounted dry if robust enough, because surface features are so much more easily seen than when mounted in a relatively high-refractive-index medium. They may be affixed in a cell between two glass slides with a minute drop of gum arabic. Transparencies may be mounted in Canada balsam or some proprietary mountant such as Euparal, which has the advantage of not requiring perfect desiccation in absolute alcohol and clearing in xylol, thus eliminating processes in which damage to the specimen may occur. Some workers prefer mounting in glycerine, which further eliminates the whole "alcohol series" and also enables the specimen to be rolled over (using a fine bristle) and viewed from different sides; but the technique of permanent mounting in glycerine presents many difficulties of its own. Storage of duplicate material, however, is always best in glycerine.

Some rhabdosomes which are too large (e.g., *Dictyonema*) or too delicate (e.g., *Rastrites*) to hold together on removal of the matrix may be cemented to a glass slide with Canada balsam or some proprietary cement after one side has been completely exposed, and when thus supported the rest of the matrix can generally be dissolved safely with HCl or HF. More recently, promising results have been obtained with blocks of polyester resins (e.g., Crystic 195 and Ceemar) in place of a glass backing (HUTT & RICKARDS, 1967). No transfer preparations can be cleared, however, as no mounting medium yet used has been found to withstand the effect of clearing reagents.

Shale material that is exceptionally well preserved (e.g., in relief in pyrite) may also be worth treating by one or other of the transfer methods described in the foregoing paragraph, and in some instances the graptolites may be sufficiently uncarbonized for complete isolation with HF and clearing, even though the stipe is completely flattened (SKOGLUND, 1961). In general, however, little can be done with specimens preserved in a shale or silt matrix beyond careful cleaning of the fossils with a fine needle under a medium-power binocular. It is sometimes an advantage, in order to gain greater contrast with the matrix, to varnish specimens after cleaning and for this purpose mastic varnish, Canada balsam, Euparal, or some similar substance may be used and can if necessary be removed later with xylol or alcohol. For subsequent examination and particularly for photography, it is desirable to cover the specimen with an ordinary microscope coverslip.

Dissolved graptolites can be embedded and sectioned with a microtome, and although HOLM satisfactorily used only paraffin wax embedding, better results can be obtained usually by double embedding in collodion and paraffin wax. Zoology technicians, much more accustomed to such procedure, usually are willing to undertake this part of the paleontologist's work.[1] Pyritized graptolites, and those preserved in limestone but too highly carbonized for any of the solution treatments, can be sectioned by serial grinding, and with a limestone matrix permanent transfers can be taken with collodion films. Restorations can be made from serial sections (microtome or grinding), either by a modification of the method of preparing block diagrams, or by drawing on glass plates, or better still as wax models, the thickness of the wax plates to be used being determined by the frequency of the sections and the magnification employed. Most generally useful, at least for proximal-end development, are reconstructions in the form of internal casts, made by cutting away a slightly exaggerated thickness of the internal and external walls, and assembling the resulting series of "thecal cavities." The result is something approaching a thecal diagram, as shown in Figures 15, 49, 62, and others.

## ILLUSTRATION

The satisfactory illustration of graptolites has always presented a difficult problem. On account of their small size, enlarged figures are necessary to show details of structure and thecal form, but illustrations at natural size are so valuable as an aid to identification that the ideal is to have both.

Enlarged figures present no special difficulties, though it should be remarked that untouched photographs are rarely satisfactory; retouched protographs or wash drawings are far preferable (for example, see Kraft, 1926, where both photographs of exceptionally high quality and wash drawings are reproduced; also excellent examples of retouched photographs in Holm's plates, Bulman, 1932-36, and of wash drawings in Wiman, 1895-1901). At high magnifications, line drawings made with a camera lucida under the microscope, or with a Shadowmaster, often leave little to be desired and can be reproduced cheaply as text figures (for example, Walker, 1953; Urbanek, 1966).

It is the natural-size figures which present the special problem, both on account of technical difficulties in reproduction and the high degree of artistic skill needed for the original drawings (for here again photographs are rarely satisfactory). The steel engravings accompanying Hall's *Graptolites of the Quebec Group*, and Törnquist's lithographic plates are alike admirable, but these methods of reproduction are now obsolete even if authors were able to emulate their drawings. Lapworth solved the problem *(Monograph of British Graptolites)* by photographic reduction of enlarged chalk and wash drawings, reproduced at natural size by a collotype process to which Messrs. Bemrose devoted special care and attention. It is doubtful whether such plates could be produced today; but since modern zinc blocks cannot reproduce satisfactorily a line drawing of a graptolite rhabdosome at natural size, and the usual halftone screens are far too coarse, some form of collotype is essential for natural-size figures.

It cannot be overemphasized that there is no substitute for well-executed wash drawings or carefully retouched photographs. Innumerable examples of modern halftone (and even collotype plates) produced from unretouched photographs at natural size or even at small magnifications serve mainly to show the limitations of this quick and labor-saving method of illustration. Because of these technical difficulties, there is inevitably a tendency nowadays to discard natural-size figures. Line drawings, reproduced as text figures with magnifications of ×2 to ×5, probably will become the standard method of illustrating the general features of a graptolite rhabdosome in future; such figures can be drawn either with a camera lucida (at ×5 to ×10) or more readily drawn on an enlarged photographic print which is subsequently bleached and reduced for reproduction. The latter method is particularly useful with large or spreading rhabdosomes, and completely supersedes use of the Lapworth microscope (described in Elles & Wood, 1901-19).

If photography is used, better results commonly are obtained by immersing the specimen in alcohol or xylol, which reduces surface reflections and increases contrast between the graptolite and surrounding matrix.

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[1] If any granules of pyrite are present in the rhabdosome, the sections are likely to be torn and there is danger of damaging the microtome knife.

## STRUCTURE AND COMPOSITION OF PERIDERM

The periderm of the Dendroidea (Kozłowski, 1938, 1949) consists of two layers, a main fusellar layer constructed of short transverse growth segments (fuselli) generally disposed with bilateral symmetry, and an outer, laminated, cortical layer (Fig. 5). A comparable structure has been demonstrated in other graptolithine orders. The fusellar layer corresponds closely in its appearance to the zooidal tubes of *Rhabdopleura* (Fig. 3) and *Cephalodiscus*. Cortical tissue is not present in *Rhabdopleura*, but is well developed in *Cephalodiscus*, and it varies greatly in amount in the Graptolithina; some dendroid and tuboid rhabdosomes exhibit so much "secondary thickening" that underlying structures are completely obscured, while even the growth lines of others remain clearly visible, and always more of it occurs at the base (proximal end) of a rhabdosome than at its distal extremities. To this extent it is a function of age.

In *Dictyonema*, the dissepiments are composed of cortical tissue. Also probably, but not certainly, the web and disc structures of some dichograptids and "float structures" of biserial graptolites are composed of cortical tissue. On the other hand, the microfusellar tissue associated with the apertures of some diplograptids and monograptids is believed to be a form of fusellar tissue. Thecal (apertural) spines are fusellar, as also is the virgella, but the exact nature of the lacinia and parts of the clathria remain obscure. Where periderm of the apertural region has been damaged or destroyed, it is replaced by tissue with normal fusellar structure, but if some area remote from an aperture is damaged, the regenerated tissue consists of a structureless membrane.

The chemical composition of the periderm of the Graptoloidea has been investigated by Florkin and his colleagues (1965). Using two species of *Pristiograptus* and one of *Climacograptus*, they have demonstrated its proteic nature and the complete absence of chitin. The presence of large amounts of serine (molecular fraction 10.6 to 22.8), alanine (6.3 to 9.5), glycine (20.1 to 23.4), aspartic acid (8.6 to 10.0) and glutamic acid (12.8 to 15.3)

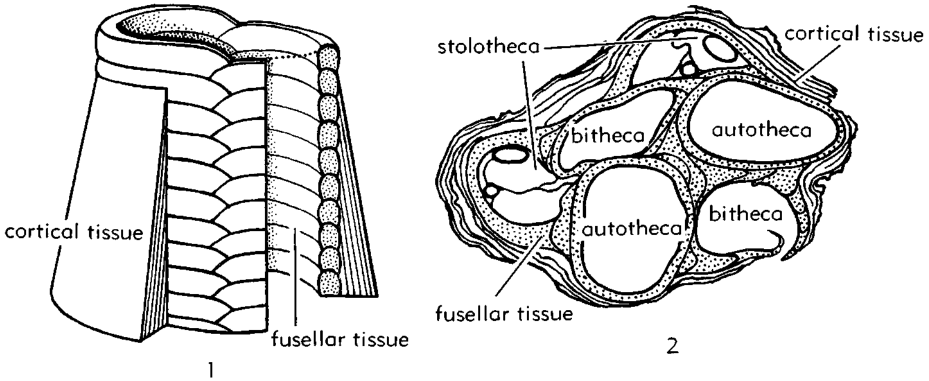

Fig. 5. Structure of graptolite periderm.

*1*. Diagram showing fusellar tissue laid down in alternating half rings, surrounded by laminated cortical tissue (114).

*2*. Transverse section of a *Koremagraptus* stipe (×130) showing cortical tissue surrounding fusellar tissue (stippled), which has the form of complete tubes for autothecae, and split tubes for bithecae and stolothecae; where growth bands are oblique (as in bitheca at lower right) many such bands are cut by the plane of the section (23).

suggests that these graptolite proteins are scleroproteic and such a composition is analogous to that of the cephalodiscoid coenoecium.

Wetzel (1958) and Kraatz (1964, 1968) have carried out some preliminary examination of thin sections of graptolite periderm at high magnifications, using the electron microscope. Wetzel indicated certain differences between the periderm of the sicula of a *Diplograptus* species and that of a *Rhabdopleura* tube. and Kraatz described several types of granular aggregates in the fusellar tissue of *Monograptus* and in the denser substance of the virgula and of a retiolitid meshwork. It is difficult at this stage to assess the significance of their findings.

## GRAPTOLITE AFFINITIES

Because the graptolites are an extinct group of animals whose soft parts have left little or no trace upon the exoskeleton, their affinities always have been in dispute. Originally regarded as inorganic (Linné, 1735) or of vegetable nature (von Bromell, 1727; Brongniart, 1828), at different times they have been assigned to the Cephalopoda (Walch, 1771; Wahlenberg, 1821; von Schlotheim, 1822), Coelenterata (Hall, 1865; Allman, 1872; Nicholson, 1872; Lapworth, 1873; Bulman, 1932), Polyzoa (Salter, 1866; Ulrich & Ruedemann, 1931), Pterobranchia (Schepotieff, 1905), or considered to occupy an isolated position in the animal kingdom not clearly related to any living group of organisms (Wiman, 1895; Perner, 1895; Ruedemann, 1895; Frech, 1897; Elles, 1922).

However, reliable and detailed description of the histology of the periderm, of its chemical composition, and nature of the stolon system now point more decisively to pterobranch affinities. The existence of fusellar and cortical layers in the periderm and the arrangement of fuselli find close parallels in the skeletal tissues of the Pterobranchia, and no other living organism has such an organ as the pectocaulus (skeletal sheath of the stolon) to which the sclerotized stolon system of the graptolites is so closely comparable. In the order Crustoidea, it is even embedded in the lower wall of the stolotheca, as in *Rhabdopleura,* though in other graptolite orders it lies free in the stolothecal tube. The proteic nature of the periderm and the absence of chitin lends additional support to this view of their affinities.

The actual method of budding seems to have been somewhat different. In *Rhabdopleura* a permanent terminal bud *("blastozooide inachevé")* is present behind which successive individuals developed from the steadily lengthening stolon, which has not distally developed its sclerotized sheath (Fig. 3); whereas in the graptolites each stolotheca in turn seems to have represented the terminal bud of its branch (Fig. 6,*1*,*2*). In the Graptoloidea, evidence for the budding of successive thecal zooids from one another is even clearer; here the prothecal segment (Fig. 6,*3*,*4*) represents the stolotheca and the stolon, assumed by analogy to have existed, lacks any skeletal sheath. These differences from *Rhabdopleura* may not be very significant; the living *Cephalodiscus,* which is placed without question within the same class as *Rhabdopleura,* have no stolon system at all and is not a truly colonial organism; and the budding processes in *Rhabdopleura* on the one hand and graptolites on the other, are closely paralleled within a single order by the monopodial and sympodial budding of calyptoblastean hydroids. Certain other differences are mentioned in the section below.

For a detailed discussion of the question of graptolite affinities, reference may be made to Kozłowski, 1966.

## NATURE OF GRAPTOLITE ZOOID

The nature of graptolite zooids is essentially conjectural, but by analogy with the pterobranchs it is now permissible to suggest a tentative restoration involving a bi-

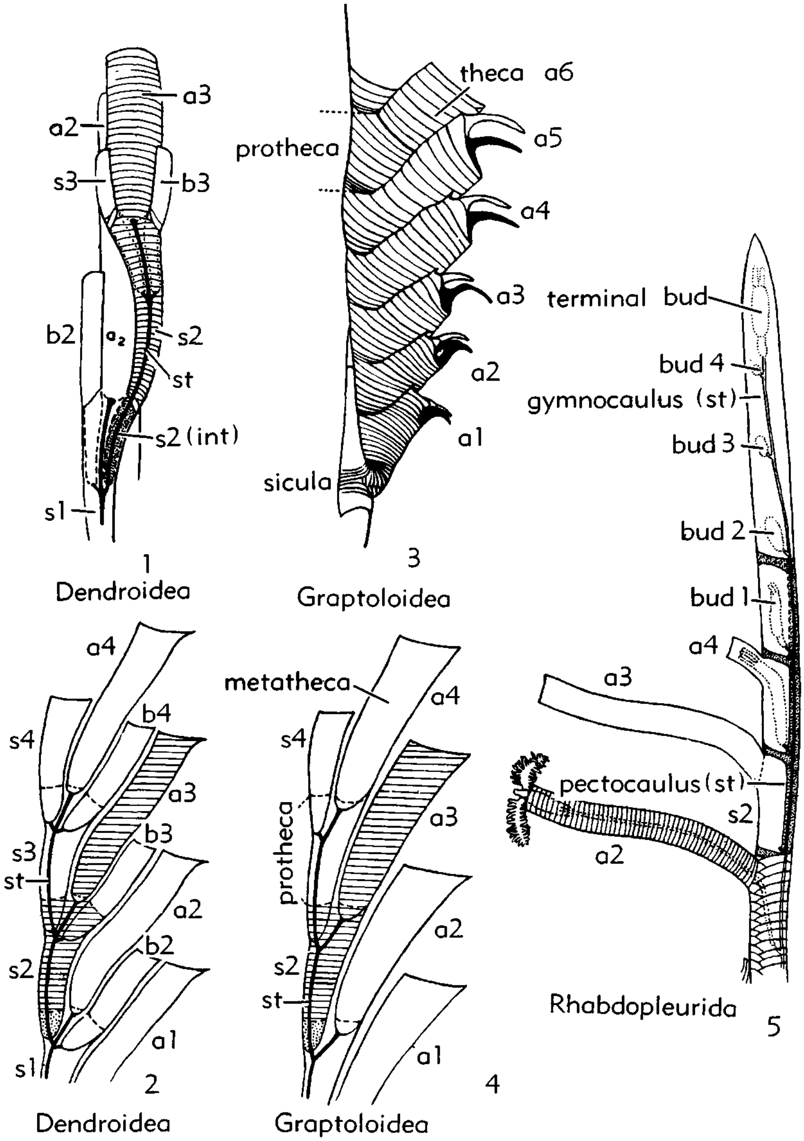

Fig. 6. Comparison of branch structure and mode of budding in Dendroidea *(1,2)*, Graptoloidea *(3,4)*, and Rhabdopleurida *(5)* (29).——*1.* Growing end of dendroid stipe (diagrammatic) with one complete autothecal unit shaded (internal portion of stolotheca stippled, external portion and daughter autotheca with growth lines).——*2-5.* Autothecal units shaded for comparison. [*a,* autotheca; *b,* bitheca; *(int),* internal portion; *s,* stolotheca; *(st),* stolon.]

lateral lophophore with two arms or groups of arms (Fig. 7). This in turn allows a convincing interpretation of some apertural modifications of the thecae, especially in the Graptoloidea, which may include spines, lobes, and even more or less tubular "hydrodynamic tunnels." Asymmetry in the apertural processes is extremely rare, but one group (cucullograptids) is characterized by the introduction of such asymmetry, and Urbanek (1966) has attributed to these highly-modified left-handed apertural structures of the extreme *Cucullograptus aversus rostratus* a hydrodynamic and supporting-protective role in relation to the hypertrophied left lobe of the lophophore (Fig. 7,*5*).

It is possible also to give some explanation, in terms of pterobranch affinities, of the polymorphism seen in many graptolite orders. Polymorphism in the coelenterate hydrosome is introduced by the presence of special reproductive or protective individuals in addition to the nourishing individuals. Likewise, the bithecae of Dendroidea at one time generally were regarded as housing such protective polyps. Dimorphism among higher organisms is prevailingly sexual and the occurrence of autothecae and bithecae on the stipes of many graptolites is now taken to indicate the presence of male and female zooids (KOZŁOWSKI, 1949, 1966b). In *Rhabdopleura* and *Cephalodiscus* males and females are usually indistinguishable externally, but certain species do show dimorphism. Thus, in *Cephalodiscus sibogae* the males are degenerate and bear an almost atrophied lophophore. The graptolite bithecae may be considered to represent such male zooids, the reduced state of their lophophore being reflected in the universal absence of apertural processes in the bithecal skeleton. The female zooids occupied the autothecae, which in several dendroid species have furnished traces of what are claimed to represent embryos (KOZŁOWSKI, 1949) and which probably possessed a well-developed lophophore as indicated by the varied apertural modifications commonly present, especially in the Graptoloidea. Disappearance of the bithecae in the Graptoloidea may imply a change to hermaphroditism, the autothecal females becoming hermaphrodite as the bithecal males were eliminated. The process may be actually visible in *Kiaerograptus,* a *Didymograptus*-like genus with bithecae regularly present distally but lacking in association with the first three of four autothecae of the rhabdosome (see Fig. 19,*3*). The existence of such forms provides a complete link between the dendroid Anisograptidae and graptoloid Dichograptidae.

In addition to these two thecal types, the Tuboidea may also exhibit microthecae, umbellate thecae, and conothecae; the first two appear to represent autothecae modified to a varying extent (and for an unknown purpose), but the conothecae differ more pronouncedly. Graptoblasts and cysts occur within the autothecae of the Crustoidea, and their interpretation also remains obscure.

It is improbable that the stolothecae contained separate zooids; indeed it is virtually

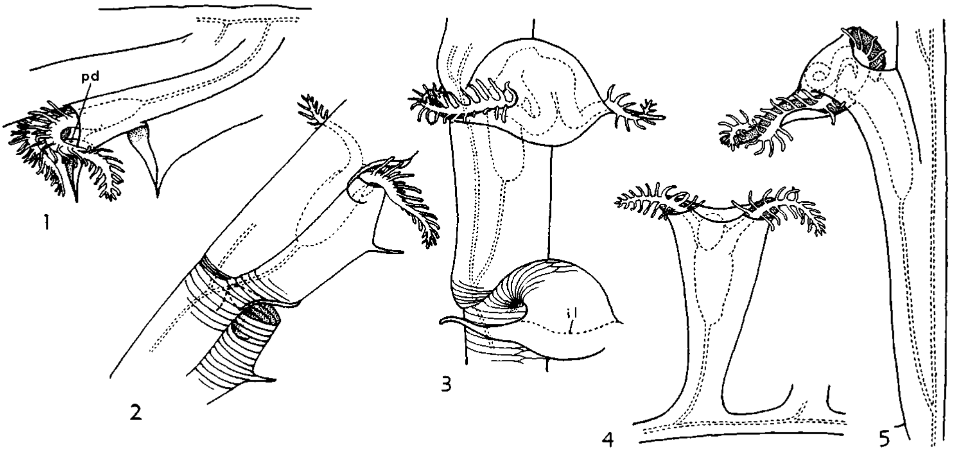

FIG. 7. Diagrammatic restorations of thecal zooids illustrating possible relations of lophophore to different types of apertural modification (Bulman, n).——*1.* Dichograptid.——*2.* Dicellograptid.——*3. Monograptus exiguus.*——*4.* Triangulate monograptid.——*5. Cucullograptus aversus rostratus.* [*il,* inner lip of aperture; *pd,* preoral disc.]

certain that in the Dendroidea each stolotheca was secreted by the same individual as the autotheca which succeeds it with continuity of periderm and without break or "unconformity" in the growth lines. Budding is thus essentially sympodial. Structural resemblances between stolothecae and bithecae (p. *V*28) are accountable on the assumption that the stolotheca was secreted by an immature autothecal zooid with the preoral lobe and lophophore still relatively undeveloped, while the bitheca was secreted by a "reduced" male in which these structures remained always undeveloped.

The laminated cortical tissue, to some extent at least invariably present among graptolites, is assumed to imply the existence of some extrathecal living tissue, possibly even enveloping the entire colony (KOZŁOWSKI, 1966b). A contrary view was expressed by BEKLEMISHEV (1951), who explained cortical tissue as the secretion of zooids which crept out of their thecal tubes just as do those of the living *Cephalodiscus,* despite the basal attachment of graptolite zooids to their stolon system. Although this is manifestly impossible in graptolites with strongly constricted thecal apertures, he contended that it could have been formed at an immature stage of thecal development while the apertural region (of the exoskeleton) was incomplete. This assumption overlooks the important fact that cortical tissue is not present distally, at the growing end of the stipe, but increases in amount proximally and can only have been deposited when the underlying thecae were mature.

The existence of this enveloping tissue constitutes a significant difference between graptolites and pterobranchs, and its relation to the body of the zooids is certainly difficult to visualize, bearing in mind that the fusellar layer of graptolites must surely have been secreted by some part of the preoral lobe. Something analogous is known to exist, however, in some Bryozoa,[1] producing an external thickening of the calcareous walls. It has been suggested (BULMAN, 1964) that this tissue may have played a role in the buoyancy of the Graptoloidea (p. *V*93), as well as in secretion and lengthening of the nema and development of "floats," webs and other extrathecal skeletal structures.

The nature of the sicular individual remains more obscure. The prosicula seems to represent the skeleton of a larva developed from a fertilized egg, originally exhibiting little trace of basal disc or nema, but possibly covered by some extrathecal membrane and either free-swimming or attached by a fleshy peduncle. This prosicular skeleton is so sharply distinct from that of the metasicula, however, that KOZŁOWSKI even believes them to have been secreted by different individuals. On this view, the prosicula corresponds to a fixed larval form, which on degeneration is replaced by a metasicular individual whose body occupied the entire cavity of the sicula to the apex of the prosicula; such a process finds some analogy in the embryonic stages of certain Polyzoa. The initial bud (or sicular stolotheca) likewise extends to the apex of the prosicula, perhaps originating as a bud from the peduncle of the metasicular zooid, and then growing up with the metasicular individual until it emerges generally through a foramen produced by resorption in the wall of the sicula in a manner comparable with the normal process of budding in *Rhabdopleura* (or less commonly through a notch as in the monograptids).

The possible role of siculozooid (the only sexually-produced individual in the colony) in controlling the pattern of rhabdosome development has been discussed by URBANEK (1960) and will be referred to more fully in the section on Graptoloidea.

# DENDROIDEA

## Order DENDROIDEA Nicholson, 1872

[*nom. transl.* RUEDEMANN, 1904, p. 578 (*ex* section Dendoidea NICHOLSON, 1872, p. 101)] [=suborder Cladophora HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 633]

Sessile Graptolithina, attached by apex of sicula, which is then generally more or less embedded in secondary cortical tissue forming a rootlike base, or more rarely attached by a nema; stipes composed of stolothecae, autothecae, and bithecae produced by regu-

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[1] R. TAVENER-SMITH (1969) recently has inferred the existence of an external, colonial mebranous investment in fenestellids.

lar triad budding; rhabdosome typically erect, dendroid in habit of growth, developed by dichotomous or irregular branching, with anastomosis or dissepimental connection between adjacent stipes in many forms; pendent to horizontal (very rarely reclined) in forms with nema attachment. *?M.Cam.*(Eng.-Nor.); *U.Cam.*(N.Am.-USSR)-*Carb.(Namur.)*(Eng.).

The Dendroidea are characterized essentially by their regular triad budding of the stolon on what has been termed the "Wiman rule," in which the autotheca constitutes the central individual at each division and the bithecae are produced alternately right- and left-handedly (Fig. 8). While this can be demonstrated conclusively in transparencies or in serial sections, it is more difficult to recognize in hand specimens, although often it can be inferred in material preserved in relief (e.g., pyritized specimens) where the triads can be detected owing to the dorsal position of the stolon system. In genera belonging to the Acanthograptidae, however, where the stipe is composed of elongate tubular individuals and the stolon system is commonly "internal," no outward indication of the budding mechanism may be seen. Exceptions to the regularly alternating triad budding are known, but are exceedingly rare.

The dendroid habit is not in itself diagnostic, since it is encountered also in the Tuboidea. Considerable uncertainty may arise therefore, both from lack of knowledge concerning fundamental generic characters and also from poor preservation of individual specimens.

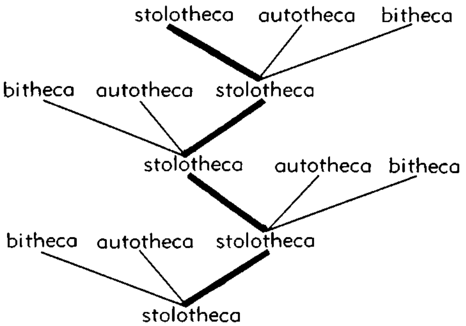

FIG. 8. Arrangement of dendroid thecae in alternating triads according to the "Wiman rule" (29).

# MORPHOLOGY

## THECAE

### STOLOTHECAE

The stolothecae of Dendroidea, formerly called "budding individuals," form a continuous closed chain lying characteristically along the dorsal side of the branch, but, in the more complex acanthograptids and inocaulids, embedded in the stipe to a greater or lesser extent. Each stolotheca terminates distally against the base of the succeeding autotheca, liberating at the same level a bitheca on one side and another stolotheca on the other (Fig. 9,*2,3*). When only this much was known about branch structure, the term "budding individual" was not inappropriate. Internally, however, each stolotheca carries a section of the sclerotized stolon system, analogous to the pectocaulus of *Rhabdopleura*. Distally, each stolotheca encloses a thin-walled proximal extension of the daughter stolotheca and bitheca, together with a long stolon from the base of the autotheca lying centrally. Traced proximally, these unite near the mid-length of the stolotheca in a stolonal triad. Globular swellings (vesicular diaphragms) may occur at the points of origin of the three thecal stolons and where the thecal stolons join the bases of their respective thecae; such diaphragms also are seen in the Crustoidea (see Fig. 26) and in certain Tuboidea. Though usually well sclerotized, the stolon system appears to have been unsclerotized in the aberrant *Graptolodendrum*.

In a typical dendroid, the growth bands of the parent stolotheca pass uninterruptedly into the base of the daughter autotheca, though a marked "unconformity" delimits growth lines at the bases of free portions of the daughter stolotheca and bitheca (Fig. 9,*2,3;* Fig. 6,*1*), indicating that in effect each stolotheca is no more than the immature basal portion of the succeeding autotheca. Clearly, no reason exists for supposing the existence of a separate stolothecal zooid. In the Tuboidea, where budding is diad, the relations are not so simple and invariable. In the Graptoloidea no sclerotized stolon system is present, but the prothecal segment of the theca undoubtedly corresponds to the dendroid stolotheca (Fig. 6,*3,4*).

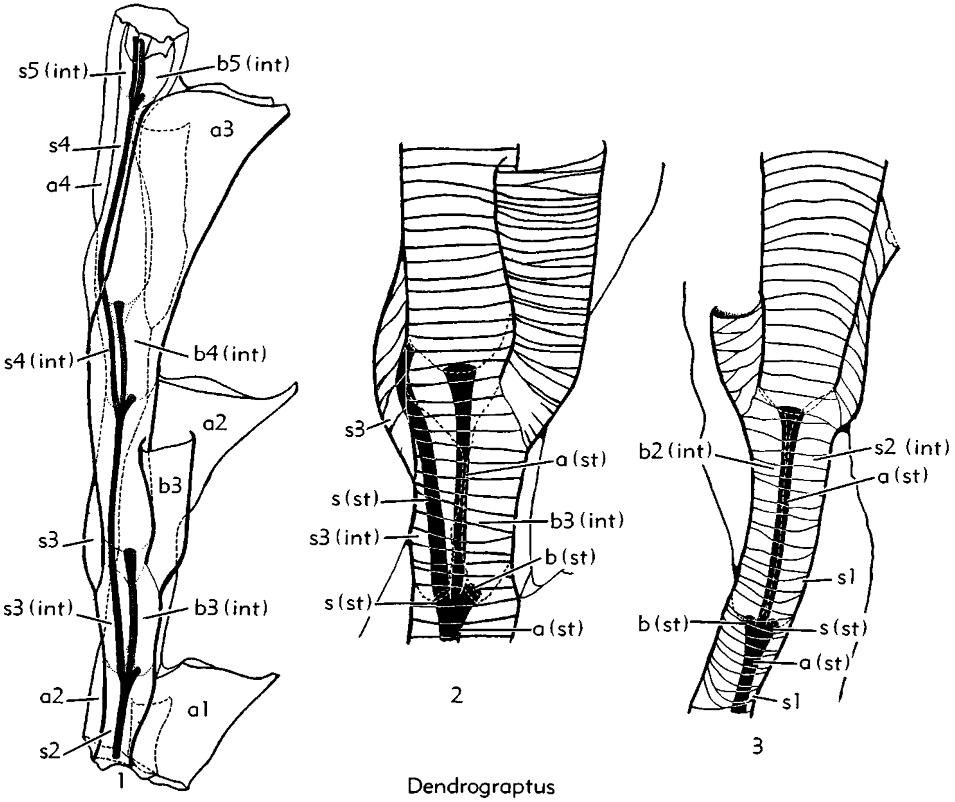

Fig. 9. Thecal constitution of a dendroid stipe (114).

1. *Dendrograptus regularis* Kozłowski (×40) viewed as transparency with growth lines omitted; stolon system in solid black, stolotheca and daughter thecae in heavy outline.
2. Portion of same with growth lines (×80).
3. *D. communis* Kozłowski (×80), distal end of branch showing immature stolotheca and bitheca. [*a,* autotheca; *b,* bitheca; *(int),* internal portion; *s,* stolotheca; *(st),* stolon.]

These relationships imply that, instead of the permanent terminal "leading bud" of *Rhabdopleura,* each autothecal zooid in turn has been the terminal zooid of its branch; the process is analogous to "sympodial budding" as compared with the "monopodial budding" of *Rhabdopleura.*

### AUTOTHECAE

The autotheca, originally called "hydrotheca," is the largest and most conspicuous of the three types of dendroid thecae, and comprises a relatively long autothecal stolon and the theca proper. The stolon and the thin, rounded base of the theca are enclosed within the stolotheca of the preceding generation, but practically the whole of what is termed autotheca is external and its dorsal wall continues that of the stolotheca uninterruptedly. The midventral line is usually marked by the zigzag wedging out of growth bands laid down alternately to right and left, and where the whole distal region of the autotheca is isolated from the branch, a similar zigzag suture line is visible on the dorsal side as well. For the most part, the autothecae are practically straight, commonly provided with an apertural (ventral) process or spine, rarely with a dorsal spine, or both. In some forms (e.g., *Dendrograptus cofeatus,* Fig. 10,*4*), this ventral process is transversely enlarged and recurved over the aperture, but the dendroid autothecae rarely exhibit apertural

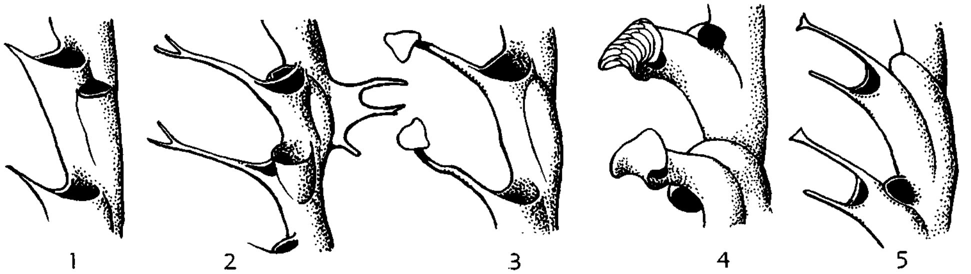

FIG. 10. Autothecal modifications in Dendroidea (29).

*1.* Apertural spine of denticle on hydrothecae of *Dictyonema flabelliforme* (EICHWALD).
*2.* Forked apertural spine of *D. cervicorne* HOLM.
*3.* Apertural spine with platelike termination in *D. peltatum* WIMAN.
*4.* Laterally expanded and reflexed ventral process (languette) shown by *Dendrograptus cofeatus* KOZŁOWSKI.
*5.* Ventral and dorsal spines in *Dictyonema rhinanthiforme* BULMAN.

modifications at all comparable with the more extreme types of elaboration shown by the Graptoloidea or Crustoidea. Some isolation of the distal end of the autotheca is by no means uncommon, accompanied by elongation of the theca reaching its extreme in the Acanthograptidae (see Fig. 21).

### BITHECAE

The bithecae are shorter and as a rule narrower than the autothecae, and are commonly inconspicuous in external view, though in some species they form marked swellings along the branch, as in *Dictyonema cervicorne,* where they were for the first time recognized by HOLM in 1890. Their wall is incomplete along the side in contact with the branch and they are without apertural spines. They further resemble the stolothecae and differ from autothecae in possessing a very short stolon and in having a long, thin-walled proximal portion which is enclosed within the stolotheca of the preceding generation.

In its simplest form, the bithecal tube is nearly straight and, owing to its shortness in comparison with the autotheca, its aperture is normally situated beside that of the autotheca of the preceding generation. A common variant is for the bitheca to open into the cavity of the preceding autotheca, when it is practically invisible in external view; other modifications, usually involving some increase in length, are shown in Figure 11. In most species the behavior of the bithecae is constant for the species, but in a few it is variable and several different types occur together, in some (e.g., *Dictyonema falciferum*) characterizing a particular portion of the rhabdosome.

### THECAL GROUPING

Regularity in triad budding is the distinctive feature of the Dendroidea, but instances of irregularity, though uncommon, are known. The Anisograptidae, essentially a transitional family linking the Dendroidea with the Graptoloidea, provide instances where the bithecae are in process of reduction or loss. Thus, bithecae are not developed in association with the proximal autothecae of the rhabdosome in *Kiaerograptus,* and in the aberrant genus *Graptolodendrum* (as in the tuboid? *Parvitubus*) the bithecae are mainly disposed along one or other side only of the branch.

The dendroid branch unit is the threefold association of autotheca, bitheca and stolotheca; and as the stolotheca does not open to the exterior (except at the growing tip of the branch) and was not inhabited by a distinct type of zooid, the effective unit is the autotheca combined with bitheca. Owing to their relative difference in length, this smaller unit is split, for the bithecal aperture is normally associated with the aperture of the autotheca of the preceding

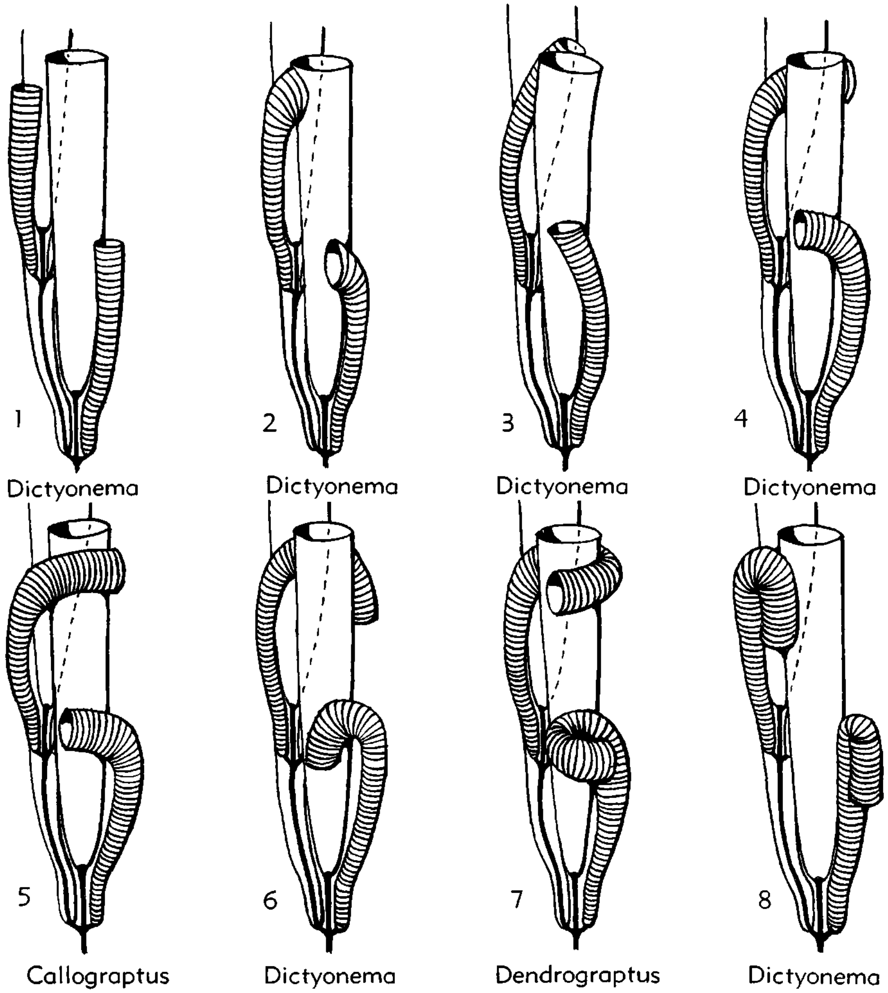

FIG. 11. Variations in form and relations of dendroid bithecae (shaded) (29).

*1. Dictyonema flabelliforme* (EICHWALD).
*2. D. peltatum* WIMAN.
*3. D. cotyledon* BULMAN.
*4. D. rarum* WIMAN.
*5. Callograptus infrabithecalis* KOZŁOWSKI.
*6. D. inconstans* BULMAN.
*7. Dendrograptus cofeatus* KOZŁOWSKI.
*8. Dictyonema wysoczkianum* KOZŁOWSKI.

generation (e.g., *bi2* opens in association with *au1*). Exceptions to this generalization are connected with elongation of the thecal tubes.

In *Pseudocallograptus* (see Fig. 17,*3*) the adnate autothecae are elongated by some 50 percent as compared with normal *Callograptus,* but the bithecae are usually of normal length, so that *bi6* opens adjacent to *au4* instead of *au5;* but irregular variations in bithecal length also occur. It is probable that comparable increase in autothecal length, altering the normal apertural association, occurs in *Pseudodictyonema* (compared with *Dictyonema*), and possibly *Stelechocladia* (compared with *Dendrograptus*), and in some species of *Desmograptus* not yet generically separated.

A distinctive elongation of the thecae characterizes members of the Acanthograptidae and may be accompanied by surprisingly regular grouping of autothecae and bithecae. This is best exhibited in *Acanthograptus suecicus,* where four variously associated thecae open together in groups or "twigs," each composed of two autothecae and two bithecae arranged as follows (Fig. 12,*1*):

twig 1: *a2, a5, b4, b5,*
twig 2: *a4, a7, b6, b7,*
twig 3: *a6, a9, b8, b9,*
and so on,

but the thecal composition of the twigs varies somewhat in different species. *A. czarnockii,* from the Tremadoc of Poland, and *A. divergens,* can be interpreted on a comparable basis though the thecal elongation is less pronounced. *A. musciformis* has more complex stipes, with more numerous thecae and more than one stolonal chain, and twigs may combine individuals derived from two or more lines of development. In *A. impar,* a cross section of the stipe may cut through as many as 30 to 35 individual tubes, of which five may be stolothecae, and though twigs are present, they tend to lose the regular fourfold grouping of simpler species. Finally, in

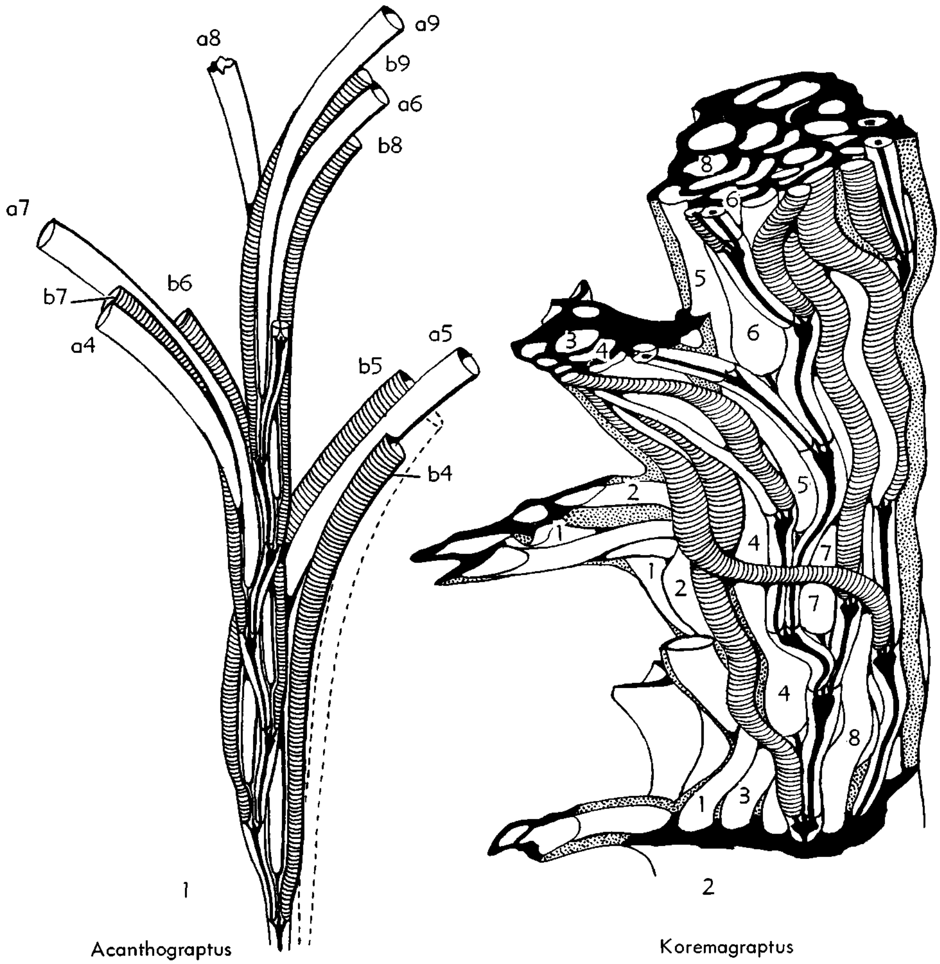

FIG. 12. Thecal grouping in the Acanthograptidae (29).

1. *Acanthograptus suecicus* (WIMAN) showing regular association of 2 autothecae and 2 bithecae to form twigs.
2. Restoration from serial sections cut by WIMAN of *Koremagraptus formosus* (WIMAN), showing complex branch with numerous main stolons and larger, more irregular, twigs (bithecae shaded; numbering of some of the autothecae only to identify such thecae as can be traced throughout the series figured).

*Koremagraptus,* with its dominant but irregular anastomosis, branchlets and twigs show little if any regularity in their construction.

## MODE OF BRANCHING

Preceding any bifurcation of a stipe, two main stolons must be produced and hence at a branching division or node two stolothecae must arise. Since the stolothecae are essentially the proximal portions of autothecae, it follows that the branching division entails production of two autothecae in place of autotheca and bitheca (i.e., the suppression of a bitheca). In spite of this, the external regularity in arrangement of the thecae along the stipe is not disturbed; slight adaptation in length of stolon and length of bitheca insures that the normal association of bithecal and autothecal apertures persists (Fig. 13,*1*), uninterruptedly.

The shape of a colony, especially a conical colony like that of *Dictyonema,* is largely dependent upon frequency of branching, but in most instances the branching divisions are uniformly scattered over the surface of the rhabdosome. However, in siculate species such as *Dictyonema flabelliforme* (Fig. 13,*2*) and in many anisograptids such as *Clonograptus* and *Anisograptus,* fairly regular "zones of branching" do appear, particularly proximally (Fig. 13,*2*), and relative lengths of various orders of branches may constitute one of the specific characters. Thus in *Anisograptus matanensis,* one of the three primary branches is about one quarter of the length of the other two, while in *A. richardsoni* all three are equal (though of different lengths from the corresponding branches of *A. flexuosus*). This suggests some degree of rhabdosomal control reminiscent of that so distinctive of the Graptoloidea. It is to be expected that branching occurs at the level of theca n±1 (as in cladia production of cyrtograptids) rather than that any particular order of branching has a precise absolute length.

Bifurcation of a complex branch containing several main stolons and elongate tubu-

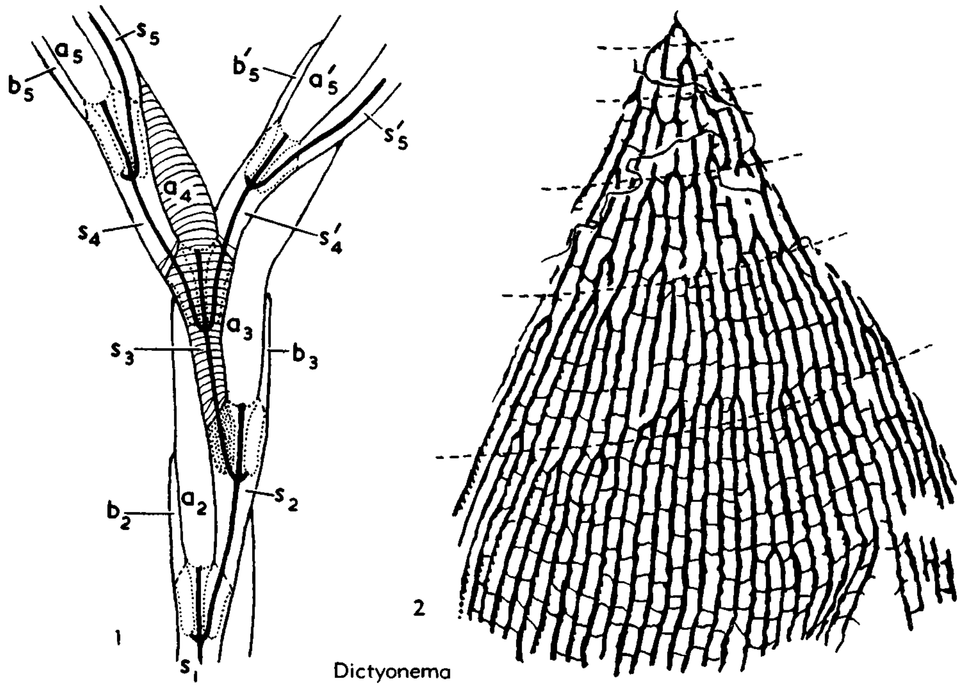

FIG. 13. Branching in *Dictyonema flabelliforme* (EICHWALD) (24).——*1.* Diagram of branching division with two stolothecae (*s4* and *s'4*) in place of stolotheca and bitheca; parent stolotheca *s3* and daughter autotheca *a4* shaded.——*2.* Approximate zones of branching in a rhabdosome of *D. flabelliforme,* ×1.

lar thecae (Fig. 12,*2*) may involve merely the separation of certain stolons, together with some associated autothecae and bithecae. Here, the technical "branching division" of the stolon involving the production of two stolothecae is not immediately related to the bifurcation of the stipe.

## DISSEPIMENTS AND ANASTOMOSIS

In *Dictyonema,* the branches are united by transverse threads called dissepiments, which may be rather erratic in spacing and direction, but in certain species are extraordinarily regular. They also characterize *Ptiograptus* and a few may be developed in certain species of *Callograptus* and even *Dendrograptus.*

These dissepiments have been shown to be extrathecal in origin and composed of cortical tissue, secreted by the extrathecal living tissue responsible for secondary thickening in general. Some exhibit growth out from adjacent branches so as to meet and fuse in the center, and two closely adjacent dissepiments may be partially or completely united by a web of cortical tissue. Two different types of mesh, one coarse, with broad widely-spaced dissepiments and the other fine, with slender closely-spaced dissepiments, may occur in the same rhabdosome in *Dictyonema flabelliforme norvegicum,* but this is exceptional. The degree of variation in dissepimental structures and mesh characters suggests need for caution in their taxonomic use.

The complicated flange structure, which produces a honeycomb appearance on the dorsal (outer) side of the rhabdosome of *Dictyonema cotyledon,* appears to be related in some way to dissepimental structures. Though apparently composed of fusellar tissue (Skevington, 1963), its formation is difficult to explain and it may prove to be a variant of the pseudofusellar cortical tissue as developed in *D. wysoczkianum.* The terminal plates on the apertural spines of *D. peltatum* may fuse to a more or less continuous sheet, but it is extremely doubtful if stipes are ever connected by apertural spines; accordingly, Ruedemann's genus *Airograptus,* based on this assumption, is not here accepted. Bithecae may grow out sporadically along dissepiments, but again no evidence is offered that regular "pseudodissepiments" are formed by bithecae or autothecae. As in the Tuboidea, however, single thecae may connect adjacent branches obliquely in *Koremagraptus,* but this is a limiting case of anastomosis prevalent in this genus.

More or less regular anastomosis characterizes *Desmograptus* and several acanthograptid and inocaulid genera, and complicated but irregular transfer of thecae, singly or in groups, may occur particularly in forms with several stolonal chains present in their branches.

## DEVELOPMENT[1]

The most detailed and complete account of dendroid development is that published by Kozłowski (1949) for *Dendrograptus communis,* which may serve as a type for the order (Fig. 14).

The prosicula is a thin-walled, almost cylindrical tube, closed and flattened at the base and usually developing a well-marked basal disc of attachment. Its walls are strengthened by a spiral thread *(Schraubenlinie, ligne helicoidale)* coiled indifferently in a clockwise or counterclockwise direction, but not exhibiting any longitudinal fibers comparable with those of the graptoloid prosicula (see Fig. 39).

From this initial prosicula, the metasicula is sharply differentiated by its closely set growth lines. These are not so strikingly regular as in the Graptoloidea, but a general zigzag line runs down the dorsal and ventral sides and the growth bands are for the most part alternating half rings, giving a definite bilateral symmetry to the metasicula. With continued growth, the metasicula of *Dendrograptus communis* begins to develop the dorsal and ventral apertural processes so conspicuous in the adult.

The initial bud or sicular stolotheca originates in a pore produced by resorption in the wall of the prosicula. After a short period of growth pressed against the wall of the prosicula and metasicula, it gives

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[1] [The general term development has been retained, in preference to astogeny, chiefly because the expressions "dichograptid type of development," "diplograptid development," etc., are by now so well entrenched in the literature. Strictly speaking, moreover, the phase covered by the term includes the ontogeny of the sicula and the astogeny of the initial part of the colony, which begins with *th1'* and comprises a small but variable number of individual thecal ontogenies.]

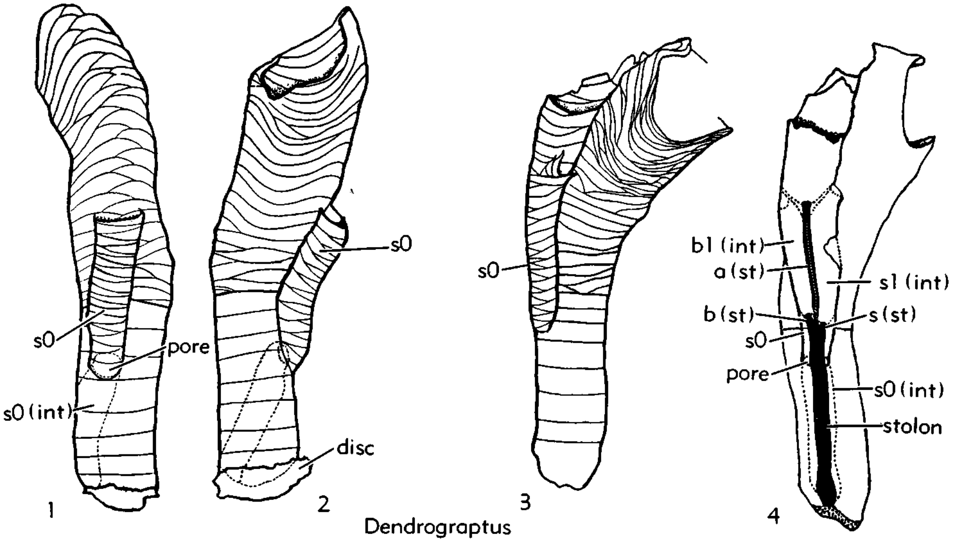

FIG. 14. Sicula and initial bud of *Dendrograptus communis* KOZŁOWSKI (114).——*1,2*. Prosicula with basal disc and spiral line, metasicula, and early stage of initial bud (stolotheca, *s0*) which extends internally *(s0int)* to base of prosicula.——*3,4*. Later stage of development showing the 3 descendants of stolotheca *0*. [All figures approx. X45; letter symbols as in Fig. 9.]

rise distally to the first triad, consisting of autotheca, bitheca, and stolotheca; proximally it can be traced within the prosicula to the basal disc as a thin-walled tube containing the initial stolon. The first triad of thecae thus produced (Fig. 14,*4*) constitutes the initial part of the main stem of the colony, which in this species extends for four or five consecutive generations before beginning to branch.

Numerous other dendroid astogenies are known in varying degrees of detail, and most agree in all essentials with that just described. The list includes: *Acanthograptus suecicus* (STRACHAN, 1959), *Calyxdendrum graptoloides* (KOZŁOWSKI, 1960), *Dictyonema flabelliforme* (BULMAN, 1949) and various anisograptids (STUBBLEFIELD, 1929; BULMAN, 1950a, 1954; SPJELDNAES, 1963), *Dictyonema cavernosum* (BULMAN & RICKARDS, 1966), *Graptolodendrum mutabile* (KOZŁOWSKI, 1966) and *Rhipidodendrum samsonowiczi* (KOZŁOWSKI, 1949). In all of these, in contrast to the Graptoloidea, the initial bud appears to be produced from the prosicula, with the exception of *Graptolodendrum,* where it originates in the metasicula. Another difference from the Graptoloidea is the absence of longitudinal strengthening fibers in the prosicula; these may be related to the development of the nema and it is possible that they occur in *Dictyonema flabelliforme* and the anisograptids, but have not yet been detected since these prosiculae are not yet known in transparencies. STUBBLEFIELD (1929) noted their possible presence in *Adelograptus hunnebergensis,* but in the late, somewhat aberrant anisograptid *Calyxdendrum* they are absent. The relation of the initial bud and earliest-formed triad of thecae tends to be indifferently right- or left-handed.

Some irregularities and departures from the typical dendroid plan begin to appear in the anisograptids, where bithecal development may become irregular. To judge from *Kiaerograptus* (SPJELDNAES, 1963), the sicular bitheca from triad *1* persists after the loss of other proximal bithecae; *Adelograptus* (SPJELDNAES, 1963) can likewise be interpreted in terms of normal dendroid development but again only the sicular bitheca has been recorded. An extraordinary astogeny was described by LEGRAND (1963) for his genus *Choristograptus,* but it is impossible to interpret the proximal end from the photographic illustrations and the genus is provisionally included here as a synonym of *Adelograptus*.

*Rhipidodendrum* (Fig. 15,*4*), which here is provisionally retained in the family Dendrograptidae, differs from typical dendroids in that the first stolonal node is diad and produces only a bitheca and a stolotheca. This is usually succeeded by one normal triad and then a concentrated series of branching divisions; this genus shows much diversity, however, and in some colonies even the second node is a branching division.

No positive evidence can be cited of any significant (genetic) relationship between two or more rhabdosomes based on a common "root system," analogous to the synrhabdosomes of the Graptoloidea. The few examples figured (*Dictyonema cavernosum* in Wiman, 1897a, and *Syrrhipidograptus* in Poulsen, 1924) are here ascribed to chance associations or a mistaken interpretation of root irregularities.

## PALEOECOLOGY

The class Graptolithina includes four orders (Tuboidea, Camaroidea, Stolonoidea, and Crustoidea) which appear to have been sessile, but concerning the ecology of which practically nothing is known. The Dendroidea, however, are somewhat better understood.

That the Dendroidea, with their thickened "stems" and discoidal or ramifying basal organs, have the morphology of sessile organisms was long ago recognized by Hall (1865). Their remains occur with other shallow-water benthonic invertebrates, and their sporadic distribution is consistent with a sessile mode of life. Few instances of attachment to shells or pebbles have ever been recorded, but the restoration attempted by Ruedemann (1925) for the Gasport lens is probably quite typical of the ecology of the group. Here are the fossilized remains of a muddy channel in the

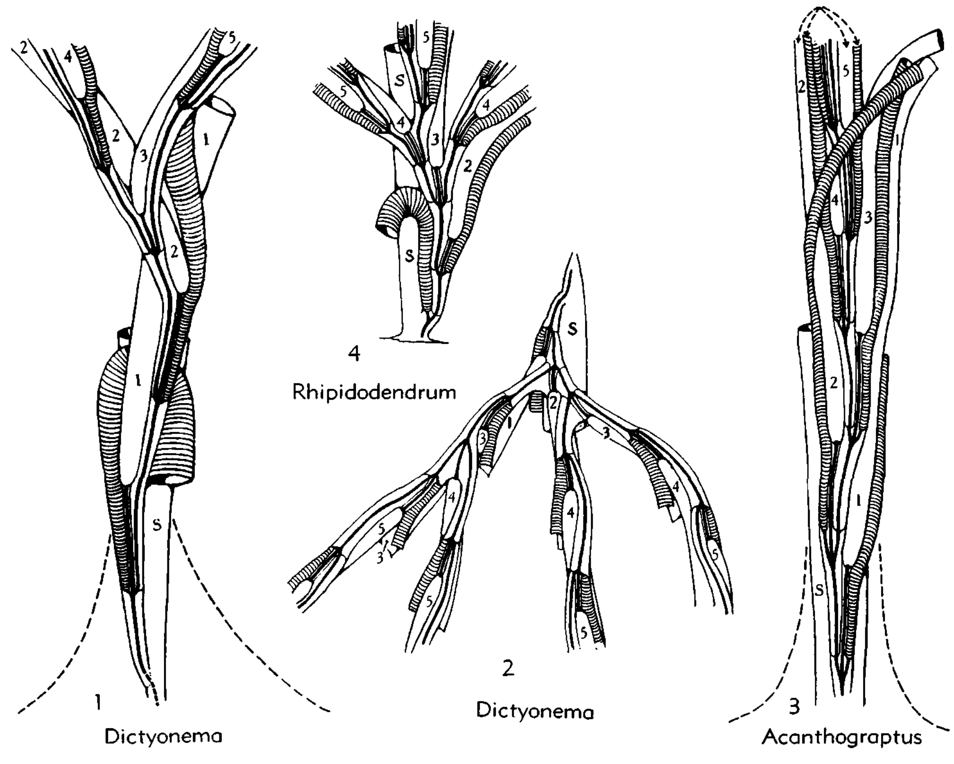

Fig. 15. Diagrams representing development of dendroid rhabdosomes (29).——*1*. *Dictyonema cavernosum* Wiman.——*2*. *D. flabelliforme* (Eichwald).——*3*. *Acanthograptus suecicus* (Wiman).——*4*. *Rhipidodendrum samsonowiczi* Kozłowski. [Autothecae numbered in order of appearance; bithecae shaded; stolon system in solid black; sicula, *S*.]

Lockport limestone sea, carpeted with a miniature forest of tough seaweed and bushy dendroid graptolites, while in the clearer water on either side up to the brink of the channel flourished a profusion of corals and crinoids, with associated brachiopods and mollusks.

This view of dendroid ecology recently has been questioned by Bouček (1957), who followed Prantl in arguing that the Dendroidea were in fact epiplanktonic, living attached to large floating algae. For example, Bouček cited particularly the occurrence of very large rhabdosomes of *Dictyonema (Pseudodictyonema) graptolithorum* in ordinary (euxinic) graptolite shales associated with *Monograptus spiralis* and *Monoclimacis vomerina.* The rootlike structure at the proximal end of most dendroids clearly does not prove attachment to the sea bottom, and structurally such forms might equally well have been attached to large floating algae. But the occurrence of dendroids in true graptolite shales is somewhat unusual and an association with the remains of benthonic organisms is more normal. Of course benthonic dendroids might have been attached to seaweed as readily as to other objects on the bottom, and if such algae broke free and drifted away (as modern *Sargassum* does), this might account for examples suggestive of epiplanktonic association. Bouček attributed the more restricted distribution of dendroids (*vis-a-vis* Graptoloidea) to the comparably more restricted occurrence of particular species of large floating algae.

Whatever view may be taken of the mode of life of the Dendroidea as a whole, an epiplanktonic existence can be attributed convincingly to such Tremadocian dendroids as *Dictyonema flabelliforme* and the Anisograptidae. These colonies probably lived attached by their nemata to floating weed, "like a bell at the end of a rope" in the words of Lapworth (1897), and it has been claimed that in adopting an epiplanktonic mode of life, *D. flabelliforme* had taken the first step along the road leading to the Graptoloidea. Strong supporting evidence here lies as much in their geographical distribution as in morphology of the proximal end; their widespread occurrence, comparable with that of the Graptoloidea, is in marked contrast to that recorded for most dendroids. The *Staurograptus* rhabdosomes attached to the alga *Sphenophycus,* described by Ruedemann (1934), are suggestive, but the possibility of a drifted association cannot be overlooked. Størmer (1933, 1935) has described and figured specimens of *Dictyonema flabelliforme* with a bladderlike structure at the proximal end; like the so-called "floats" of the Graptoloidea (p. V93), these structures are perhaps more likely to have supported vesicular tissue than to be themselves air bladders, but such forms would appear to have become truly planktonic.

## GEOGRAPHIC DISTRIBUTION

Many dendroid genera (e.g., *Dictyonema, Dendrograptus, Desmograptus*) certainly have an extremely wide if not a world-wide distribution, but few species appear to have any notable geographic range. Bouček (1957) rightly pointed out that the dendroids are still very inadequately described and that few critical comparisons between materials from different areas are available, so that generalizations are dangerous. But of the rich dendroid fauna comprising some 50 species described by Spencer (1884) and Bassler (1909) from the Niagaran of Hamilton, Ontario, less than half have been reported from even nearby localities in the United States, and an extremely small proportion from other continents. Bouček (1957) monographed over 90 dendroid species from the Silurian of Bohemia, of which more than 80 are new (or can be referred to species already described by Počta); only six of these are referred to Niagaran forms, and two to species from other European countries. In the present state of knowledge, it can be said surely that the geographical distribution of species of dendroid graptolites is restricted as compared with graptoloid species, and this would accord with a sessile, benthonic mode of life.

## STRATIGRAPHIC DISTRIBUTION

A species attributed to *Dendrograptus* has been described by Öpik (1933) from the Middle Cambrian (*Paradoxides davidis*

Zone) of Norway, and an undescribed form is known from the same horizon in the Middle Cambrian of Shropshire, England. In addition to these, a number of Graptolithina (e.g., *Siberiodendrum, Dithecodendrum*) of uncertain taxonomic position (possibly representing a new order, but possibly dendroid or tuboid) have been described from the Middle Cambrian of Siberia, USSR, by OBUT (1964). Apart from these records, the earliest occurrence of the Dendroidea is in the Upper Cambrian; RUEDEMANN (1933) described a small fauna, including species of *Dendrograptus, Callograptus* and *Dictyonema,* from the Trempealeauan Stage of Wisconsin and a somewhat larger fauna (poorly illustrated) has been described from the Wilberns Formation of Texas by DECKER (1945). Other occurrences have been described from Quebec and from western Canada, and although it is possible that some of these records may be tuboid rather than dendroid, with little doubt dendroid graptolites were well established by Late Cambrian times. From then they persist with remarkably little conspicuous change to the Carboniferous, the highest dendroid being perhaps an undescribed species of *Dictyonema* from the Yoredale Series of Yorkshire, England. The time range of many individual genera is also extremely long; both *Dictyonema* and *Callograptus* extend from Upper Cambrian to Carboniferous, *Desmograptus* from Lower Ordovician (Arenig) to Carboniferous, and *Dendrograptus* from ?Middle or Upper Cambrian to Upper Silurian. Most genera range through the Ordovician and Silurian.

## CLASSIFICATION

With the gradual accumulation of morphological detail, a satisfactory basis for classification of the Dendroidea may emerge, but at present, when the structure of certain species of a few genera is known in great detail while the majority are still "form genera," a conservative attitude has been adopted here in recognizing both families and genera. A large number of genera, including many newly described ones, have been relegated to *incertae sedis,* or, where it appears difficult to maintain their individuality on the basis of gross morphology, they have been classed as synonyms.

The distinction between the Acanthograptidae and Inocaulidae, accepted in the first edition of this *Treatise,* has now been abandoned. The structure of *Inocaulis* remains practically unknown (and even triad budding is as yet unproved), and from the point of view of gross morphology it appears to differ from *Acanthograptus* essentially in degree: the thecal tubes have become so slender as to be capillary. Again, the differences between *Palaeodictyota* and *Thallograptus* are scarcely such as to justify allocation to two separate families, and both can only be assigned familial and even ordinal position with reservation. To this extent, the broad classification adopted here agrees with that proposed by BOUČEK (1957), except that he erected a separate order for *Inocaulis* (to which he also assigned *Medusaegraptus* and *Palmatophycus*).

Indifferent preservation naturally creates uncertainty. A poorly preserved *Koremagraptus,* for example, could be indistinguishable from the tuboid *Reticulograptus;* the generic identification of particular species, like individual specimens, must remain provisional in perhaps the majority of instances.

The predominantly Tremadocian family Anisograptidae, which appeared originally to comprise a number of genera plausibly derived from perhaps a single species of siculate *Dictyonema,* has been extended to include the mid-Ordovician *Calyxdendrum,* which must have acquired its siculate character independently and at a much later date. Moreover, even the Tremadocian anisograptids now appear to be probably polyphyletic.

## SYSTEMATIC DESCRIPTIONS

### Family DENDROGRAPTIDAE Roemer in Frech, 1897

[Dendrograptidae ROEMER in FRECH, 1897, p. 568]

Rhabdosome conical, flabellate, or irregularly dendroid, usually with thecate or more or less thickened nonthecate stem terminating proximally in rootlike processes or disc of attachment, rarely attached by nema; branching generally dichotomous, stipes free or united by anastomosis or by transverse dissepiments. Autothecae denticulate to tubular and isolate, commonly with unpaired apertural spine or process, inwardly facing in conical rhabdosomes; bithecae variable in form, usually inconspicuous externally; stolothecae situated on dorsal side of stipe. *?M.Cam., U.Cam.-Carb.*

The branches of dendrograptids are characteristically simple, with relatively short and denticulate autothecae, and even where these are more elongate and isolate,

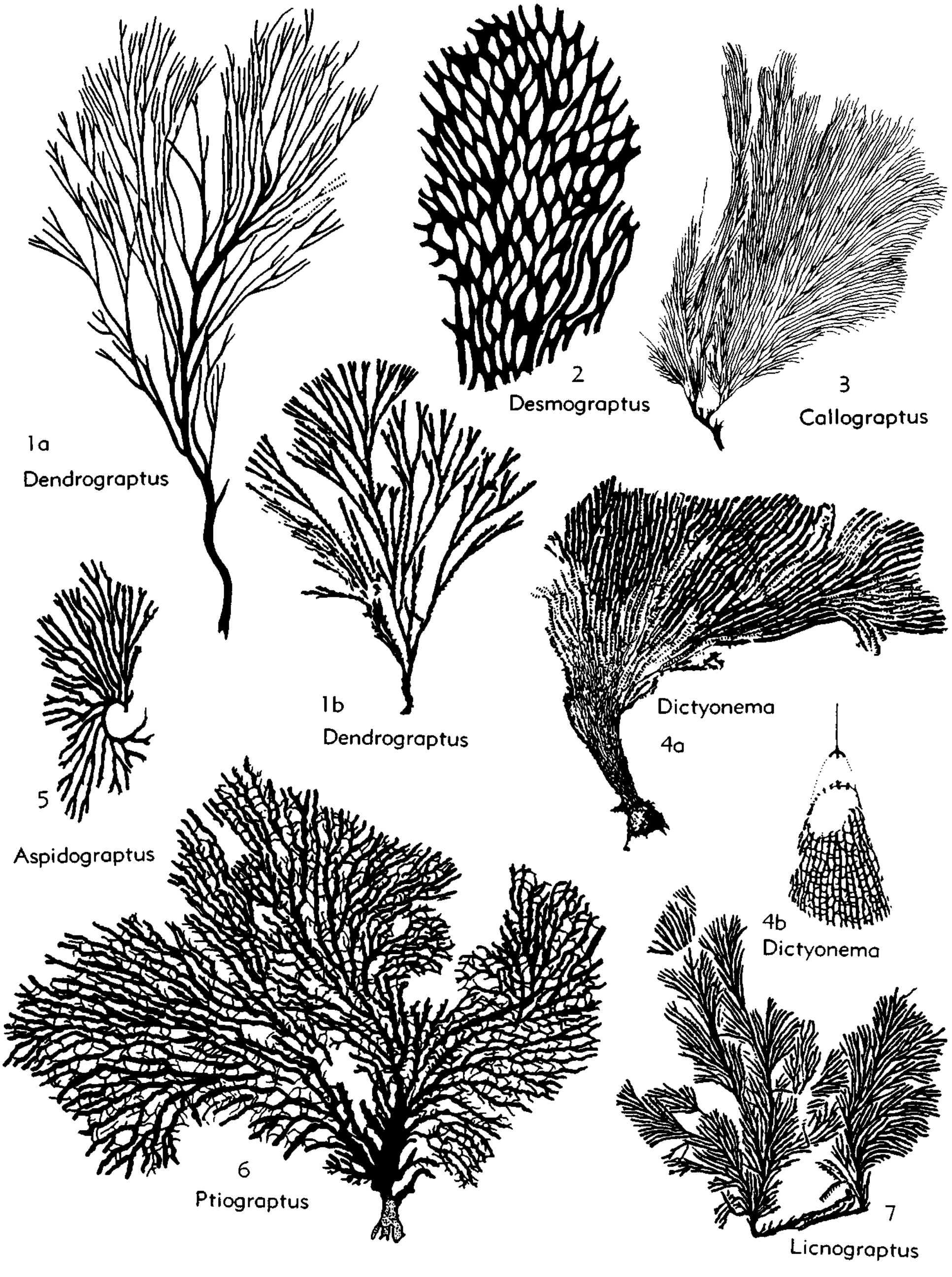

Fig. 16. Dendrograptidae (p. *V*38-*V*39).

their apertures are all directed ventrally in a single row, with the single stolonal chain on the dorsal side of the branch.

**Dendrograptus** Hall, 1858, p. 143 [**Graptolithus hallianus* Prout, 1851, p. 189; SD Hall, 1862, p. 21] [=?*Ophiograptus* Poulsen, 1937, p. 24 (type, *O. inexpectans;* OD)]. Generally robust, shrublike in habit, branching irregularly, stipes usually divergent, unconnected, stem well developed, with basal attachment; autothecae denticulate, spined or with apertural processes. *?M.Cam., U.Cam.-Carb.,* almost worldwide.——Fig. 16,*1a*. *D. fruticosus* Hall, L.Ord.(Levis Sh.), Que.; ×1 (77).——Fig. 16,*1b*. **D. hallianus* (Prout), U.Cam.(Trempeal.), Minn.; ×1 (209).

[It is probable that *Stelechocladia* Počta, 1894, p. 206 (*emend.* Bouček, 1957, p. 35, type, *S. fruticosa* Počta, 1894, p. 207; SD Bouček, 1957, p. 35 (=*Dendrograptus (Stelechocladia) suffruticosus* Bouček, 1957, *nom. nov.*, p. 36); =?*Callodendrograptus* Decker, 1945, p. 28, type, *C. sellardsi;* OD) is a subgenus bearing the same relation to *Dendrograptus* that *Pseudocallograptus* does to *Callograptus.*]

**Aspidograptus** Bulman, 1934, p. 70 [**Clematograptus implicatus* Hopkinson, 1875, p. 652; OD]. Similar to *Dendrograptus* but branching laterally from ?4 curved principal stipes; lateral branches close-set, irregularly produced, bifurcating repeatedly. *U. Cam.-Ord.,* Eu.-N.Am.-S.Am.-China.——Fig. 16,*5*. **A. implicatus* (Hopkinson), L.Ord.(Arenig), Eng.; ×1 (18).

**Callograptus** Hall, 1865, p. 133 [**C. elegans;* SD Miller, 1889, p. 175] [=*Odontocaulis* Lapworth, 1881, p. 175 (type, *O. keepingi;* OD); *Capillograptus* Bouček, 1957, p. 46 (type, *Callograptus dichotomus* Počta, 1894, p. 182; M)]. Rhabdosome conical, flabellate or somewhat irregular, with the thecae stem (*Odontocaulis* condition) or more usually thickened nonthecate stem, branching dichotomously with some regularity, stipes subparallel to parallel, sporadically united by anastomosis or dissepiments. *U.Cam.-Carb.,* almost worldwide.

**C. (Callograptus).** Autothecae denticulate, rarely isolate distally, with normal length ratio; apertural processes in some developed into acute spines. *U.Cam.-Carb.,* almost worldwide.——Fig. 16,*3*. **C. elegans,* Levis Sh., Can.(Que.); ×0.75 (77).

**C. (Alternograptus)** Bouček, 1956, p. 131 [**C. (A.) holubi;* OD]. Proximal branching lateral, stipes alternating to left and right, distal branching normal, dichotomous. *L. Ord.(Arenig),* Eu.(Czech.).——Fig. 17,*1*. **C. (A.) holubi,* Klabava beds, Rokycany; proximal portion of rhabdosome, ×2 (11).

**C. (Pseudocallograptus)** Skevington, 1963, p. 19 [**Callograptus salteri* Hall, 1865, p. 135; OD]. Autothecae and bithecae elongate, producing "ropy" appearance of stipe and unusual association of thecal apertures; autothecae generally denticulate. *L.Ord.,* Eu.-N.Am.-S.Am.——Fig. 17,*3*. *C. (P.)* cf. *C. (P.) salteri* (Hall), Vaginatumkalk (Ontikan),Sweden(Öland); fragment of stipe showing thecal elongation, ×14 (214). [*a,* autotheca;; *bi,* bitheca; *st,* stolotheca].

**Desmograptus** Hopkinson, in Hopkinson & Lapworth, 1875, p. 668 [**Dictyograptus cancellatus* Hopkinson, 1875, p. 668; M] [=*Rhizograptus* Spencer, 1878, p. 460 (*pro Rhizograpsus* Spencer, 1878, ICZN Opin. 650) (type, *R. bulbosus;* M); ?*Syrrhipidograptus* Poulsen, 1924, p. 1 (type, *S. nathorsti*; M)]. Rhabdosome conical, possibly flabellate rarely, stipes flexuous, united by regular anastomosis and rare dissepiments; autothecae denticulate to isolate. *L.Ord.(?Tremadoc)-Carb.,* Eu.-N.Am.——Fig. 16,*2*. **D. cancellatus* (Hopkinson), Arenig Sh., S.Wales; ×1 (95).

[It is possible that species with strongly isolate thecae should be grouped together under the name *Syrrhipidograptus* Poulsen, 1924, bearing the same relation to *Desmograptus* that *Pseudocallograptus* does to *Callograptus.*]

**Dictyonema** Hall, 1851, p. 401 [**Gorgonia retiformis* Hall, 1843, p. 115; SD Miller, 1889, p. 185] [=*Phyllograpta* Angelin, 1854, p. iv (type, *Gorgonia flabelliformis* Eichwald, 1840, p. 207; M); *Rhabdinopora* Eichwald, 1855, p. 453 (type, *Gorgonia flabelliformis* Eichwald, 1840, p. 207; SD Bulman, herein); *Graptopora* Salter, 1858, p. 65 (type, *G. socialis;* M); *Dictyograptus* Hopkinson, 1875, p. 667 (*pro Dictyonema* Hall); *Damesograptus* Jahn, 1892, p. 645 (type, *Dictyonema* sp. Dames, 1873, p. 383; OD); *Dictyodendron* Westergård, 1909, p. 62 (*pro Dictyonema ex D. flabelliforme*); *Dictyograptus* Westergård, 1909, p. 63 (type, *Gorgonia flabelliformis* Eich-

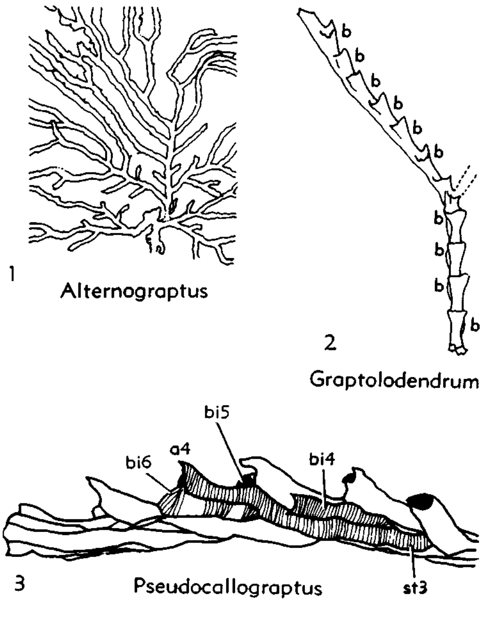

Fig. 17. Dendrograptidae [*a,* autotheca; *b, bi,* bitheca; *st,* stolotheca] (p. *V*38-*V*39).

WALD, 1840, p. 207; OD); *Airograptus* RUEDEMANN, 1916, p. 20 (type, *Dictyonema furciferum* RUEDEMANN, 1904, p. 606; OD); *Nephelograptus* RUEDEMANN, 1947, p. 196 (type, *N. rectibrachiatus;* OD)]. Rhabdosome conical, varying from almost cylindrical to almost discoidal, with thecate or nonthecate stem or rarely attached by nema; branching dichotomous, stipes straight, subparallel to parallel, united by transverse dissepiments, anastomosis rare; autothecae denticulate, commonly spined, rarely tubular and isolate; bithecae normally inconspicuous. *U.Cam.-Carb.,* almost worldwide.

**D. (Dictyonema).** Autothecae denticulate, with normal length ratio. *U.Cam.-Carb.,* almost worldwide.——FIG. 16,*4a*. *D. (D.) crassibasale* BASSLER, Sil.(Niag.), Hamilton, Ont.; ×1 (5).——FIG. 16,*4b*. *D. (D.) flabelliforme* (EICHWALD), L.Ord.(Tremadoc), Pedwardine, Eng.; ×1 (18).

**D. (Pseudodictyonema)** BOUČEK, 1957, p. 69 [**Dictyonema graptolithorum* POČTA, 1894, p. 196; OD]. Autothecae and bithecae elongate, producing "ropy" appearance of stipe; apertures denticulate or slightly isolate. *U.Sil.,* Eu. (Czech.).

**Graptolodendrum** KOZŁOWSKI, 1966, p. 4 [**G. mutabile;* OD]. Similar to *Dendrograptus* but with abnormal bithecae, mainly on one side of stipe only, and other abnormalities in detailed structure. *L.Ord.,* Eu.(Pol.).——FIG. 17,*2*. **G. mutabile,* glacial boulder (*?Glyptograptus teretiusculus Zone*); *b* indicates side (left or right) on which bithecae occur; ×5 (123).

**Licnograptus** RUEDEMANN, 1947, p. 196 [**L. elegans;* OD]. Several principal branches bearing fanlike groups of subparallel branches laterally and distally; thecal details unknown. *L.Ord.,* Can.(Que.-Newf.).——FIG. 16,*7*. **L. elegans,* Levis Sh., Que.; ×1 (209).

**Ptiograptus** RUEDEMANN, 1908, p. 175 [**P. percorrugatus;* OD]. Like *Dictyonema* but rhabdosome flabellate; dissepiments irregular, commonly angular; thecal details unknown. *Sil.-L.Carb.,* N.Am.-NW.Eu.——FIG. 16,*6*. **P. percorrugatus,* M.Dev., Ky.; ×1 (201).

**Rhipidodendrum** KOZŁOWSKI, 1949, p. 133 [**R. samsonowiczi;* OD]. Rhabdosome minute, fan-shaped, branching irregularly from 3 primary branches; autothecae and bithecae tubular, conspicuously curved. *L.Ord.-(Tremadoc),* Eu.(Pol.).

**Sagenograptus** OBUT & SOBOLEVSKAYA, 1962, p. 74 [**S. gagarini;* M]. Somewhat similar to *Dictyonema,* but with coarse irregular meshwork. *L. Ord.,* USSR(Taimyr).

## Family ANISOGRAPTIDAE Bulman, 1950

[Anisograptidae BULMAN, 1950, p. 79]

Rhabdosome siculate, pendent to horizontal or rarely reclined, quadriradiate, triradiate or bilateral; branching usually dichotomous, rarely lateral; stipes with typical dendroid structure, autothecae and bithecae characteristically simple, the latter reduced and partially absent in some, stolonal chains dorsal, superficial. *L.Ord. (Tremadoc), ?U.Ord.(Nemagraptus gracilis Zone).*

**Anisograptus** RUEDEMANN, 1937, p. 61 [**A. matanensis;* OD]. Rhabdosome triradiate, developed by dichotomous division to 6th order (usually 3rd or 4th) from 3 primary branches; typically horizontal but including declined and slightly reclined forms; autothecae denticulate, bithecae short, simple. *L.Ord.(Tremadoc),* N.Am.-S.Am.-NW.Eu.-USSR-N.Afr.(Morocco).——FIG. 18,*4*. **A. matanensis,* Matane Sh., Que.; ×1 (25).

**Adelograptus** BULMAN, 1941, p. 114 [**Bryograptus? hunnebergensis* MOBERG, 1892, p. 92; OD] [=*?Choristograptus* LEGRAND, 1963, p. 52 (type, *C. louhai;* OD)]. Usually declined or almost horizontal, rarely pendent, commonly somewhat lax and flexuous, developed from 2 primary stipes by infrequent and irregular branching, apparently lateral rather than dichotomous; autothecae denticulate, bithecae and stolothecae in geologically early species. *L.Ord.(Tremadoc-Arenig),* NW. Eu.-N.Am.-USSR-N.Afr.(Alg.)-N.Z.-Australia.——FIG. 18,*3*. **A. hunnebergensis* (MOBERG), Tremadoc, Eng.; ×1 (229).

**Aletograptus** OBUT & SOBOLEVSKAYA, 1962, p. 76 [**A. hyperboreus;* M]. Rhabdosome quadriradiate, comprising 4 undivided primary stipes; thecal structure unknown. *L.Ord.(Tremadoc),* USSR (Taimyr).

**Bryograptus** LAPWORTH, 1880, p. 164 [**B. kjerulfi;* SD GURLEY, 1896, p. 64]. Rhabdosome pendent to declined, developed from 3 primary stipes by irregular and apparently lateral branching; stolothecae and bithecae present in geologically early species. *L.Ord.(Tremadoc-Arenig),* NW.Eu.-N. Am.-N.Afr.-Australia-?China.——FIG. 18,*2a*. **B. kjerulfi,* Tremadoc, Sweden; ×1 (257).——FIG. 18,*2b*. *B. patens* MATTHEW, Tremadoc, Que.; ×1 (25).

**Calyxdendrum** KOZŁOWSKI, 1960, p. 109 [**C. graptoloides;* OD]. Rhabdosome minute, pendent, dendroid, branching at close intervals; autothecae conical, bithecae opening into autothecal cavities; prosicula lacking longitudinal fibers, but with relatively thick nema. *?U.Ord.(Nemagraptus gracilis Zone),* glacial boulders, Eu.(Pol.).——FIG. 19,*1*. **C. graptoloides,* proximal end; ×35 (119). [*a1, a2,* etc., autothecae; *b1, b2,* etc., bithecae; *n,* nema; *si,* sicula; *s0, s1,* etc., stolothecae.]

**Clonograptus** NICHOLSON (*ex* HALL MS), 1873, p. 138 [*pro Clonograpsus* HALL & NICHOLSON, 1873, ICZN, Opin. 650] [**Graptolithus rigidus* HALL, 1858, p. 146; SD Miller, 1889, p. 179] [=?*Herrmannograptus* Monsen, 1937, p. 186 (type, *Graptolithus milesi* Hall, 1861, p. 372; OD)]. Rhabdosome bilateral, produced by dichotomous division, generally at steadily increasing intervals, to 8th or 9th order (usually 5th or 6th); branches diverging proximally, becoming subparallel, and in some species flexuous, distally; autothecae denticulate with moderate inclination, some species with low inclination and negligible overlap, some with exaggerated apertural spines; stolothecae and bithecae in geologically early species; central disc and web structures rare. [In view of the variability of *Clonograptus,* it seems scarcely feasible to maintain *Herrmannograptus* Monsen, 1937, as a distinct genus.] *L.Ord.(Tremadoc-Llanvirn),* almost

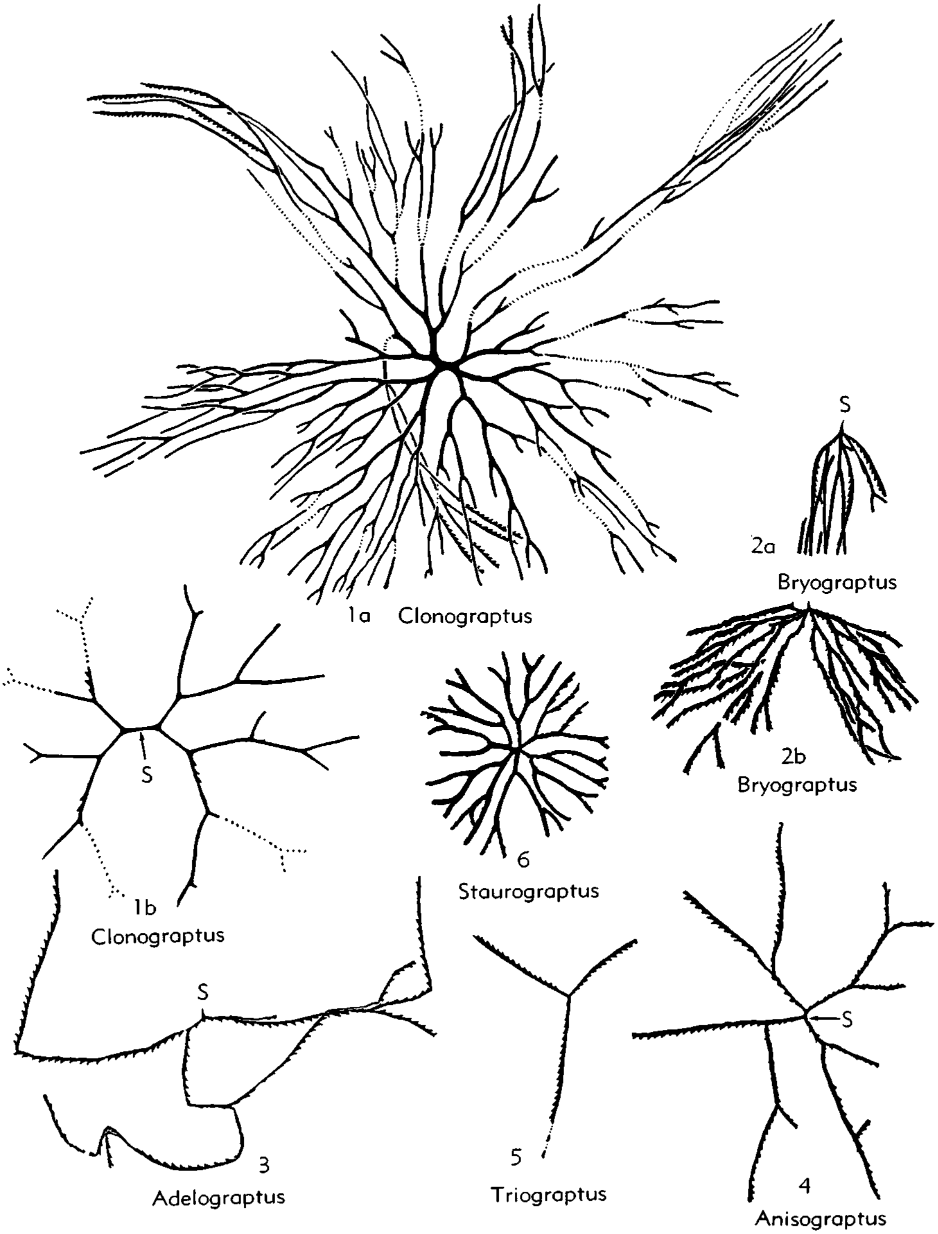

FIG. 18. Anisograptidae [*S*, sicula] (p. *V*39-*V*41).

worldwide.——Fig. 18,*1a*. *C. flexilis* (Hall), Levis Sh., Que.; ×0.5 (78).——Fig. 18,*1b*. *C. tenellus* Linnarsson, Tremadoc, S.Sweden; ×1 (144).

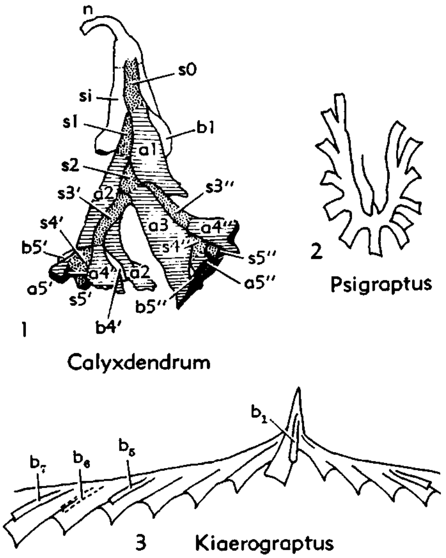

Fig. 19. Anisograptidae [*a*, autotheca; *b*, bitheca; *n*, nema; *s*, stolotheca; *si*, sicula] (p. *V*39-*V*41).

**Kiaerograptus** Spjeldnaes, 1963, p. 123 [**Didymograptus kiaeri* Monsen, 1925, p. 172; OD]. Rhabdosome bilateral, composed of 2 undivided, horizontal stipes; autothecae of dichograptid type, bithecae present distally. *L.Ord.(Tremadoc)*, Eu.(Norway)-?N.Am.——Fig. 19,*3*. **K. kiaeri* (Monsen), Norway; [*b1*, etc., bithecae], ×5 (Bulman, n).

**Psigraptus** Jackson, 1967, p. 314 [**P. arcticus;* OD]. Rhabdosome siculate, composed of 2 (or ?3) short, reclined stipes; autothecae distally isolate, stolothecae and bithecae believed present. *L. Ord.(Tremadoc)*, N.Am.(Yukon).——Fig. 19,*2*. **P. arcticus*, Rock River; ×4 (105).

**Radiograptus** Bulman (*ex* Lapworth MS), 1950, p. 89 [**R. rosieranus;* OD]. Rhabdosome triradiate, discoidal, composed of numerous branches dividing dichotomously, connected by sparsely developed dissepiments; thecal structure imperfectly known. *L.Ord.(Tremadoc)*, N.Am.(Que.).

**Staurograptus** Emmons, 1855, p. 108 [*pro Staurograpsus* Emmons, 1885, ICZN, Opin. 650] [**S. dichotomous;* M]. Rhabdosome small, quadriradiate, developed by dichotomous division to about 4th order of 4 primary stipes, typically horizontal; bithecae imperfectly known. [Genus is commonly almost indistinguishable from discoidally preserved immature specimens of *Dictyonema* and it possibly has no validity.] *L.Ord. (Tremadoc)*, N.Am.-Australia-?NW.Eu.——Fig. 18,*6*. **S. dichotomus*, Schaghticoke Sh., N.Y.; ×1 (201).

**Triograptus** Monsen, 1925, p. 169 [**T. osloensis;* M]. Rhabdosome triradiate, composed of 3 horizontal, undivided stipes; stolothecae and bithecae present. *L.Ord.(Tremadoc)*, NW.Eu.-N. Am.——Fig. 18,*5*. *T. canadensis* Bulman, Matane Sh., Que.; ×1 (25).

## Family PTILOGRAPTIDAE Hopkinson in Hopkinson & Lapworth, 1875

[Ptilograptidae Hopkinson in Hopkinson & Lapworth, 1875, p. 661]

Rhabdosome sessile, dendroid, with alternating pinnate arrangement of lateral branches. *L.Ord.-U.Sil.*

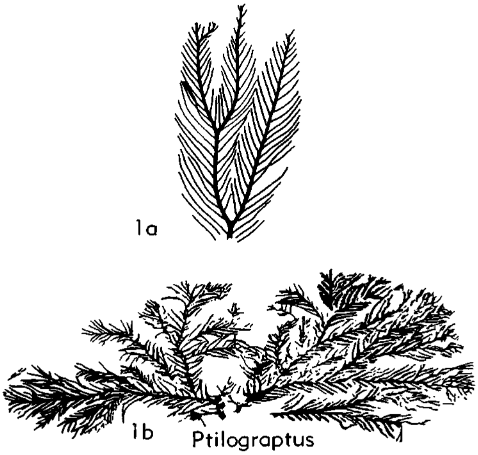

Fig. 20. Ptilograptidae (p. *V*41).

**Ptilograptus** Hall, 1865, p. 139 [**P. plumosus;* SD Miller, 1889, p. 201] [=*Denticulograptus* Schmidt, 1939, p. 122 (type, *Ptilograptus acutus* Hopkinson & Lapworth, 1875; OD)]. Rhabdosome with comparatively few main branches, bifurcating rarely and bearing closely set lateral branches arranged alternately on opposite sides; autothecae usually denticulate, but thecal details and constitution almost unknown. *L.Ord. (Arenig)-U.Sil.*, Eu.-N.Am.-Australia. —— Fig. 20,*1a*. **P. plumosus*, L.Ord.(Levis Sh.), Que.; ×1 (77).——Fig. 20,*1b*. *P. delicatulus* Ruedemann, Ord.(Ottosee Sh.), Tenn., ×1 (209).

## Family ACANTHOGRAPTIDAE Bulman, 1938

[Acanthograptidae Bulman, 1938, p. 20]
[Incl. Inocaulidae Ruedemann, 1947, p. 230]

Rhabdosome sessile, conical to irregularly dendroid; stipes flexuous and anastomosing or rigid and irregularly branching, composed of elongate, tubular and in some forms almost capillary thecae, adnate proximally and isolate distally to varying extent, produced in normal dendroid triads but commonly showing distinctive grouping; stipes generally compound, with several stolonal chains enclosed within each branch. *?U.Cam., L.Ord.-M.Dev.*

**Acanthograptus** Spencer, 1878, p. 461 [*pro Acanthograpsus* Spencer, 1878, ICZN, Opin. 650] [**A. granti;* M] [=*?Boučekocaulis* Obut, 1960, p. 148 (type, *Acanthograptus jubatus* Obut, 1953; OD)]. Robust dendroid rhabdosome composed of rather stout branches bifurcating irregularly; very rarely anastomosing; thecae elongate, tubular, isolate distally to produce spinous appearance of branch; minor branches or "twigs" usually composed of 2 autothecae and 2 bithecae. *?U.Cam.,*

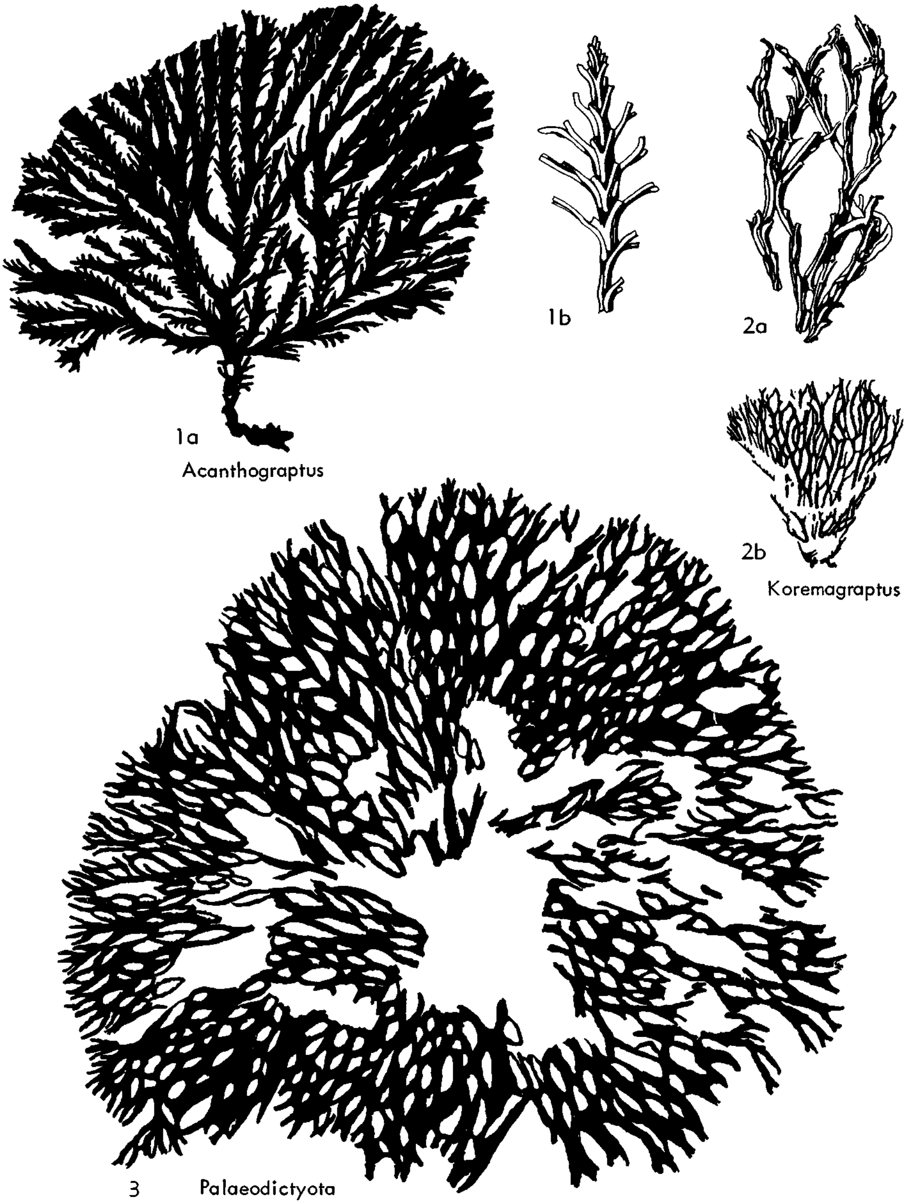

Fig. 21. Acanthograptidae (p. *V*42-*V*43).

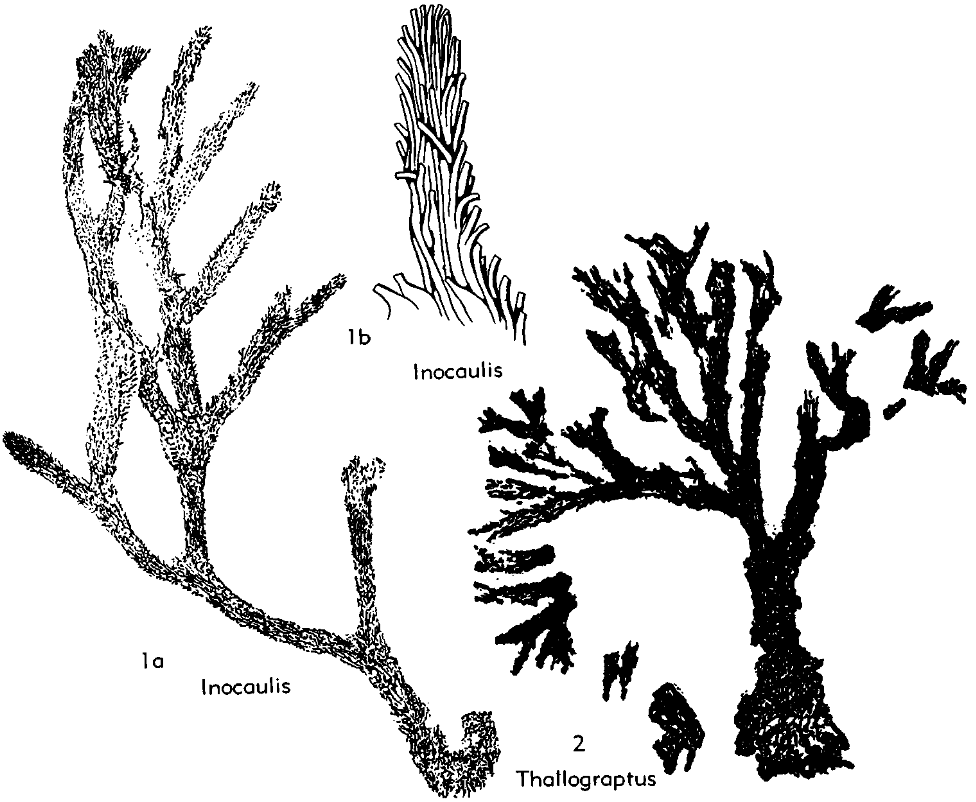

Fig. 22. Acanthograptidae (p. *V*42-*V*43).

*L.Ord.-U.Sil.,* Eu.-N.Am.-Asia-Australia.——Fig. 21,*1a*. **A. granti,* M.Sil.(Niag.), Ont.; ×1 (201). ——Fig. 21,*1b*. *A. musciformis* (Wiman), U. Ord., Baltic; distal part of branch, ×7 (267).

**Inocaulis** Hall, 1852, p. 176 [**I. plumulosa;* M]. Very thick branches, bifurcating irregularly, composed of extremely fine, capillary thecae projecting distally as hairlike processes. *Sil.,* Eu.-N.Am.——Fig. 22,*1*. **I. plumulosa,* Niag., Ont.; *1a,* ×1; *1b,* distal fragment of stipe, ×5 *(1a,*5; *1b,*201).

**Koremagraptus** Bulman, 1927, p. 345 [* *K. onniensis;* M] [=*Coremagraptus* Bulman, 1942, p. 285 *(nom. van.); Trimerohydra* Kozłowski, 1959, p. 217 (type, *T. glabra;* OD); *Dyadograptus* Obut, 1960, p. 147 (type, *D. praecursor;* OD); *Archaeodictyota* Obut & Sobolevskaya, 1967, p. 55 (type, *A. dragunovi;* OD)]. Rhabdosome conical or flabellate; branches complex, with several stolonal chains, particularly in species from higher stratigraphical levels; branches and "twigs" anastomosing irregularly; thecae very long, tubular, usually adnate for much of their length. *?U.Cam., L.Ord.-M.Dev.,* Eu.-USSR.——Fig. 21,*2b*. **K. onniensis,* L.Sil.(U.Llandovery), Eng.; ×1 (17).——Fig. 21,*2a*. *K. kozlowskii* Bulman, U.Ord.(Balclatchie beds), S.Scot., showing tubular thecae and "twigs"; ×6 (23).

**Palaeodictyota** Whitfield, 1902, p. 399 [**Inocaulis ramulosus* Whitfield (*non* Spencer, 1884), =*I. anastomoticus* Ringueberg, 1888, p. 131; SD Ruedemann, 1908, p. 200]. Resembling *Koremagraptus,* but without projecting thecae and twigs; branches probably composite but stolonal system unknown. *Sil.-M.Dev.,* N.Am.-Eu.——Fig. 21,*3*. **P. anastomotica* (Ringueberg), Sil. (Rochester Sh.), N.Y.; ×1 (201).

**Thallograptus** Ruedemann, 1925, p. 35 [*non Thallograptus* Öpik, 1928] [**Dendrograptus? succulentus* Ruedemann, 1904, p. 581; OD] [=*?Calyptograptus* Spencer, 1878, p. 459 *(pro Calyptograpsus* Spencer, 1878, ICZN, Opin. 650) (type, *C. cyathiformis;* SD Miller, 1889, p. 175)]. Like *Acanthograptus,* but with more numerous and slender thecae, the isolate distal ends of which are rarely preserved; branch structure unknown. *Ord.-Sil.,* N.Am.-Eu.-USSR. ——Fig. 22,*2*. *T. cervicornis* (Spencer), M.Sil. (Rochester Sh.), N.Y.; ×1 (203).

# TUBOIDEA

## Order TUBOIDEA Kozłowski, 1938

[Tuboidea Kozłowski, 1938, p. 185] [Introduced by Kozłowski in 1938 without diagnosis but descriptive notes in text; defined by Bulman (21) in 1938, p. 92, but first adequately described by Kozłowski (114) in 1949, p. 140]

Sessile Graptolithina, with erect stipes and more or less dendroid rhabdosomes, or encrusting, with terminally erect thecae or sheaves of thecae arising from basal disc or thecorhiza; stolothecae less prominent than in Dendroidea, generally confined to basal disc in forms with thecorhiza; autothecae and bithecae present, budding commonly diad, with no regular succession and variably spaced nodes; specially modified autothecae (microthecae and umbellate thecae) and conothecae may occur. *?U.Cam., L. Ord.-Sil.*

Like the Dendroidea, the Tuboidea are characterized by the presence of stolothecae, autothecae, and bithecae, but their association, arrangement and succession is far less regular. In the Dendroidea, with uniform triad budding, it is possible to regard the stolothecae as immature autothecae, but in the Tuboidea the relationship is not so simple; the terminal individual of a long chain of diad buds may be an autotheca, conotheca, or bitheca.

The two families recognized by Kozłowski in 1949 are possibly not so sharply delimited as they originally appeared to be, and *Dendrotubus? erraticus* Kozłowski and *Parvitubus* Skevington are to some degree intermediate. It is probable that several families are involved here, for the range of forms assigned to the Tuboidea is increasing and many now classed as dendroids (or *incertae sedis*) may prove to be tuboid. However, structural details are as yet insufficiently known to provide a reliable classification and the two original families are provisionally retained here; distinction between them rests mainly upon the dominantly dendroid habit of the Tubidendridae and the discoidal encrusting nature of the Idiotubidae.

## MORPHOLOGY

The general form of the entire rhabdosome varies from an essentially dendroid, possibly flabellate, form to an encrusting assemblage of thecae (thecorhiza) from which tubular autothecae arise singly or in groups or sheaves.

In dendroid forms adjacent stipes may be connected by anastomosis or by transfer of single thecae (autothecae or bithecae) simulating dissepiments. Autothecae commonly open on one ("inner") side. Bithecae are more abundant than autothecae and the spacing and positioning of their apertures is less regular. Conothecae, when present, are quite irregular and development of the tubidendrid rhabdosome is as yet unknown.

In encrusting forms, stolothecae and bithecae are typically confined to the thecorhiza, but in some forms provisionally included in the family, sheaves of thecae (branches) may include stolothecae and bithecae; such sheaves divide infrequently, however, and are not of dendroid habit.

## THECAE

### STOLOTHECAE

In *Tubidendrum,* the stolon system is well developed, the stolons being provided with thick, well-sclerotized and strongly pigmented walls; but in *Reticulograptus,* sclerotized stolons have not been observed within the stolothecae, even though autothecal and bithecal stolons can be recognized. Instead of occupying the external position characteristic of typical Dendroidea, the stolothecae are commonly embedded in the stipe and several stolonal chains are usually present in a single stipe. Stolonal budding is diad (Fig. 23) in a manner associating any pair of thecae except two autothecae; but all divisions producing a conotheca appear to mark the end of a particular stolonal chain, the other individual being a bitheca. Stolothecae are of variable length and no regular budding rhythm is observed. Their distribution in thecorhizate forms appears to be quite irregular.

### AUTOTHECAE

The autothecae are elongate and tubular, varying considerably in length and produced from autothecal stolons which also vary greatly in length. Despite this, the

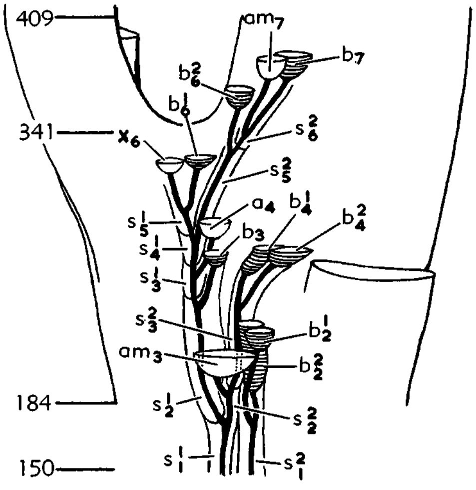

FIG. 23. Stolon system of *Tubidendrum* (solid black, with bases only of daughter thecae) reconstructed from and lettered as in serial sections figured by KOZŁOWSKI (114, pl. 21). [*a*, autotheca; *am*, microtheca; *b*, bitheca; *s*, stolotheca; sections 150-409.]

autothecal openings on branches or sheaves may exhibit surprising regularity in spacing. Ventral and, less commonly, dorsal apertural spines or processes may be present and the whole apertural region may be distinctly isolate.

In *Tubidendrum*, the autothecae are remarkable for the coiling of their central portions (Fig. 24) into a helical spiral with some seven or more turns. This coiling, either right- or left-handed, is so tight as to produce a columella analogous to that of a turreted gastropod shell. In one measured example, the autothecal stolon was 175μ long, the proximal portion of the autotheca 1,315μ, the coiled portion (measured along the axis) 620μ, and the straight distal portion 250μ. These coiled thecae, nevertheless, are enveloped in the stipe. Autothecal dimorphism occurs in *Tubidendrum*, one type (called **microthecae**) having a narrow terminal portion about one-third the diameter of a normal autotheca, with an oblique aperture which faces the opposite side of the stipe from that of the normal autotheca; in other respects, form and dimensions are comparable.

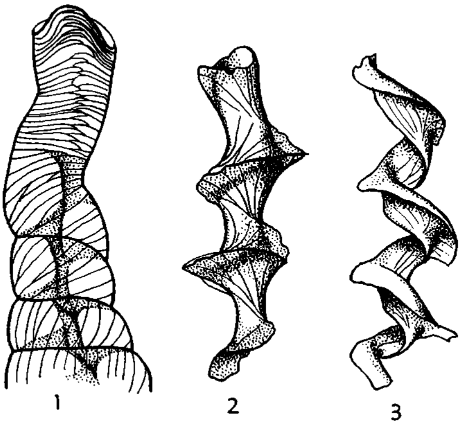

FIG. 24. Structural features of *Tubidendrum* (114).——*1*. Coiled and distal portions of an autotheca, ×40.——*2,3*. Examples of columella from the helicoidal parts of 2 autothecae, ×90.

In the encrusting forms, each autotheca characteristically comprises two portions, a proximal adnate part incorporated in the thecorhiza and an erect distal part, free or associated in a sheaf with other thecae. Probably merely because both organisms are encrusting, the general characters are not unlike those of *Rhabdopleura*. The basal portion incorporated in the thecorhiza consists of regular growth bands of fusellar tissue on its upper surface, but the lower surface is a structureless membrane. The erect portion, however, is composed of regular growth bands disposed right and left, forming two (dorsal and ventral) zigzag sutures. Near the base of this free portion, the autotheca may show some helical Coiling (see Fig. 28,*1*) comparable on a smaller scale with that of *Tubidendrum*. Autothecae produced from stolothecae in the branches *(Dendrotubus? erraticus)* are of a generalized cylindrical form. In *Galeograptus*, autothecae are also dimorphic, those on the proximal portions of the branching sheaves possessing elaborate apertural modifications; these **umbellate** thecae (Fig. 25,*1*) develop an umbrella-shaped structure shielding the aperture of the preceding theca, and the shields fill the cavity formed by the ring of stipes in the proximal region with a vesicular mass of skeletal tissue.

### BITHECAE

It is a distinctive feature of the branching tuboids that the bithecae are about twice as numerous as the autothecae and are irregularly positioned. The majority

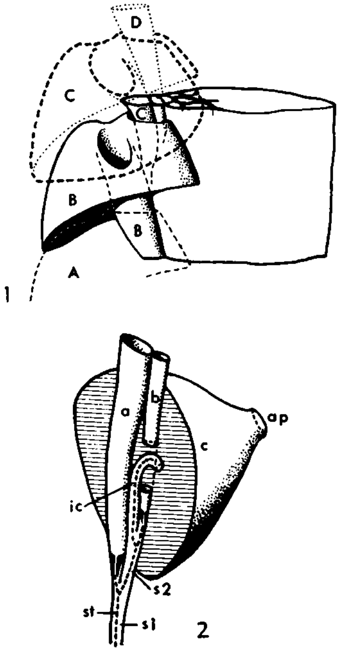

FIG. 25,*1,2*.——*1*. Diagrammatic figure of portion of stipe of *Galeograptus* showing umbellate thecae *A, B, C,* each with apertural process shielding the preceding thecal aperture; *D* is the proximal portion of the 4th theca; approx. ×25 (37).——*2*. Diagrammatic figure of conotheca of *Reticulograptus,* approx. ×30 (37). [*a,* autotheca; *ap,* aperture; *b,* bitheca; *c,* conotheca; *ic,* internal portion of conotheca; *s1, s2,* stolothecae; *st,* main stolon.]

have small relatively inconspicuous apertures almost flush with the surface of the stipe, but slight isolation may occur and some few may constitute "pseudodissepiments," transferring to and opening on an adjacent branch. Bithecal stolons vary in length, but are generally considerably longer than in the Dendroidea. In encrusting rhabdosomes, bithecae in general are limited to the thecorhiza and their numerical relation to autothecae is unknown.

### CONOTHECAE

Conspicuous conelike bodies with a small aperture at the apex of the cone occur in several tuboid genera (Fig. 25,*2*). Their detailed morphology is imperfectly known, but they arise from a thin-walled cylindrical proximal portion, enclosed within the cone, and no sclerotized stolon has been detected. In branched rhabdosomes (e.g., *Reticulograptus*) they occur at irregular and often widely-spaced intervals, and the stolonal division producing a conotheca seem to terminate the stolon chain, since the other theca appears invariably to be a bitheca. Conothecae also have been detected on the thecorhiza of *Discograptus* and *Idiotubus.*

## FORM OF RHABDOSOME AND THECAL GROUPING

A graded morphological series leads from *Idiotubus,* with autothecae arising singly from the upper surface of the thecorhiza, through *Dendrotubus* and *Discograptus,* with autothecae concentrated into groups, to *Galeograptus* and *Cyclograptus,* with a peripheral concentration of large sheaves of autothecae and bithecae. The same series illustrates also a progressive increase in regularity with which the thecae are distributed. In *Idiotubus,* the erect portions of the autothecae appear to have been distributed quite haphazardly over the surface of the thecorhiza; in *Dendrotubus* the arrangement is generally irregular but with a tendency towards greater regularity at the distal ends of the thecal bundles. In *Discograptus,* the thecae are arranged more precisely along several radii, steadily increasing in height peripherally, and the outer circle of sheaves comprise a series of autothecae regularly increasing in length and with regularly spaced apertures. In *Galeograptus* and *Cyclograptus,* the stipes are confined to the periphery and are composed of very numerous thecae with bithecal apertures concentrated around their bases or occurring on the branches themselves. Differences in the stolonal systems underlying these varied groupings are at present unknown. *Dendrotubus? erraticus* shows a tendency toward an irregularly branched tubidendrid rhabdosome rather than the unbranched radial groupings of *Galeograptus.*

## DEVELOPMENT[1]

Development of a tuboid rhabdosome recently has been described (KOZŁOWSKI, 1963) in a form provisionally referred to *Dendrotubus* (Fig. 26). A slender, erect metasicula arises from a prosicula shaped apically like a conical flask. A pore, formed

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[1] *See* footnoe on page *V32.*

in the prosicula after formation of the metasicula is complete, transmits the stolon system, and the astogeny is spiral, either right- or left-handed. Where the initial "prostolon" reaches the prosicular wall two almost spherical vesicular diaphragms originate the first stolonal and thecal stolons, and this first theca is apparently a bitheca. Subsequent diad divisions, always with vesicular diaphragms, are shown diagrammatically in Figure 26. No other tuboid astogeny is known, but the erect cylindrical metasicula has been identified in a central position in *Discograptus,* where some indication of a comparable spiral development also occurs.

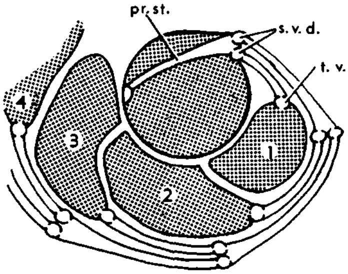

FIG. 26. Diagrammatic illustration of astogeny of *Dendrotubus* (122). [*pr.st.,* prostolon in circular basal portion of sicula; *s.v.d.,* vesicular diaphragms at base of stolons; *t.v.d.,* vesicular diaphragms at base of thecae; *1,2,3,4,* adnate basal portions of successive thecae.].

## SYSTEMATIC DESCRIPTIONS

### Family TUBIDENDRIDAE Kozłowski, 1949

[Tubidendridae KOZŁOWSKI, 1949, p. 160]

Rhabdosome erect, conical or ?flabellate; stipes dividing irregularly and anastomosing or united by single thecae, comprising at any given level numerous thecae of several generations; stolothecae more or less embedded in the stipe; autothecae tubular or spirally coiled in middle portion, dimorphism in one genus, one type (microthecae) with contracted apertural region; conothecae present in one genus; bithecae tubular with stolons of variable length; stolon system well developed and sometimes highly sclerotized. *L.Ord.(Tremadoc)-Sil.*

**Tubidendrum** KOZŁOWSKI, 1949, p. 160 [**T. bulmani;* OD]. Rhabdosome an irregular network, branches connected by tubular thecae, especially bithecae; autothecae helically coiled, dimorphic (autothecae and microthecae). *L.Ord.(Tremadoc),* Eu.(Pol.).——FIG. 24,*1-3.* **T. bulmani; 1,* autotheca, ×40; *2,3,* columellae, ×90 (114).

**Reticulograptus** WIMAN, 1901, p. 189 [**Dictyonema tuberosum* WIMAN, 1895; M] [=*Multitubus* SKEVINGTON, 1963, p. 51 (type, *M. spinosus;* OD); =?*Marsipograptus* RUEDEMANN, 1936, p. 385 (type, *M. bullatus;* OD)]. Branches anastomosing or connected by tubular thecae; autothecae with regularly spaced apertures; conothecae commonly present. *L.Ord.-Sil.(Wenlock),* Baltic-N.Am.——FIG. 27,*1.* **R. tuberosus* (WIMAN), U.Ord. boulder, Gotl.; thecal composition diagram of portion of stipe; ×20 (37).——FIG. 27,*2,3. R. thorsteinssoni* BULMAN & RICKARDS, Sil., Canad.Arctic; *2,* portion of stipe with numerous bithecae; *3,* portion of stipe with conothecae; ×20 (37).

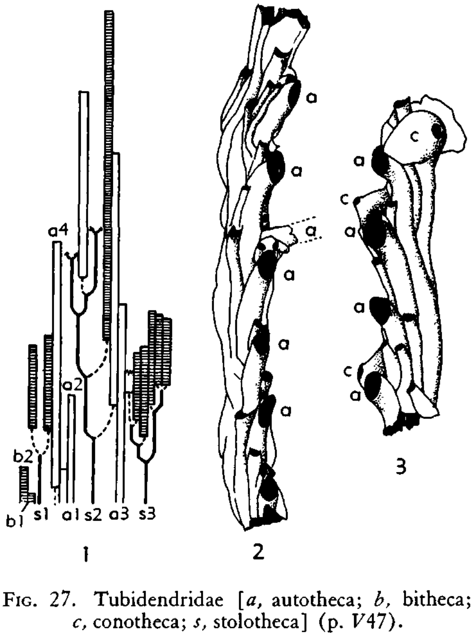

FIG. 27. Tubidendridae [*a,* autotheca; *b,* bitheca; *c,* conotheca; *s,* stolotheca] (p. *V*47).

### Family IDIOTUBIDAE Kozłowski, 1949

[Idiotubidae KOZŁOWSKI, 1949, p. 144]

Rhabdosome an encrusting, more or less discoidal assemblage of thecae (thecorhiza) from which tubular thecae arise singly or in groups or sheaves; stolothecae mainly confined to thecorhiza; proximal portion of at least initial autothecae incorporated in

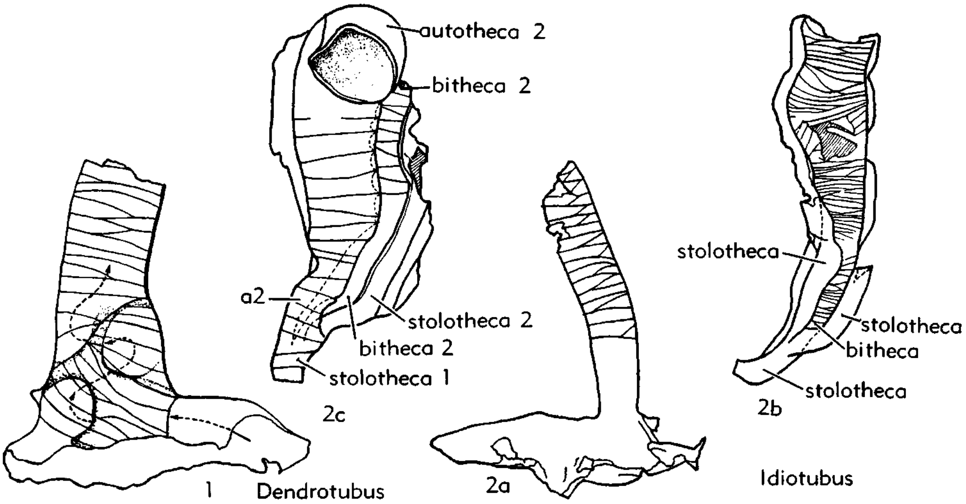

FIG. 28. Idiotubidae (p. V48).

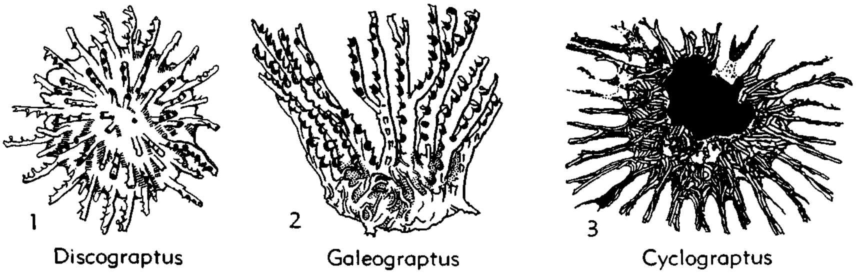

FIG. 29. Idiotubidae (p. V48-V49).

thecorhiza, distal portion tubular, erect; umbellate thecae present in one genus, conothecae in two genera; bithecae limited to thecorhiza or extending into thecal sheaves, rarely originating on branches. *?U.Cam.*(USSR), *U.Ord.-Sil.*

**Idiotubus** Kozłowski, 1949, p. 144 [**I. typicalis;* OD]. Irregularly distributed erect portions of autothecae arising singly from surface of thecorhiza. *L.Ord.(Tremadoc),* Eu.(Pol.).——FIG. 28,*2*. *I.* sp.; *2a,* autotheca and fragment of thecorhiza, ×25; *2b,* bitheca with stolothecae, ×25; *2c,* autotheca with associated bitheca and stolothecae, ×50 (114).

**Calycotubus** Kozłowski, 1949, p. 156 [**C. infundibulatus;* OD]. Autothecae fused by their lateral walls into irregular groups. *L.Ord.(Tremadoc),* Eu.(Pol.).

**Conitubus** Kozłowski, 1949, p. 159 [**C. siculoides;* OD]. Known only by conical autothecae. *L.Ord.(Tremadoc),* Eu.(Pol.).

**Cyclograptus** Spencer, 1883, p. 365 [**C. rotadentatus* Spencer, 1884, p. 42; M] [=*Rhodonograptus* Počta, 1894, p. 205 (type, *R. astericus,* =*Sphaerococcites scharyanus* Goeppert, 1860, p. 454; M)]. Rhabdosome discodial, erect portions of autothecae grouped into 20 to 30 peripheral sheaves bifurcating at their mid-length. *M.Sil. (Niag.-Wenlock),* N.Am.-Eu.(Czech.). —— FIG. 29,*3*. **C. rotadentatus,* Hamilton, Ont.; ×2 (26).

**Dendrotubus** Kozłowski, 1949, p. 153 [**D. wimani;* OD]. Erect portions of autothecae forming irregularly distributed groups, central portions commonly coiled into helical spiral. *L.Ord. (Tremadoc),* Eu.(Pol.).——FIG. 28,*1*. **D. wimani;* basal part of autotheca showing spiral coiling; ×65 (114).

**Discograptus** Wiman, 1901, p. 191 [**D. schmidti;* M]. Rhabdosome discoidal, erect portions of autothecae in more or less radially arranged groups on upper surface of thecorhiza; bithecae and conothecae confined to thecorhiza. *U.Ord.,* Baltic. ——FIG. 29,*1*. **D. schmidti,* silicified boulders, Gotland; ×3 (267).

**Epigraptus** Eisenack, 1941, p. 24 [**E. bidens;*

M]. Similar to *Idiotubus*. *Ord.(Wesenberg F.)*, Eu.(Estonia).

?**Fasciculitubus** Obut & Sobolevskaya, 1967a, p. 56 [**F. tubularis;* OD]. Robust thecae arising in irregular groups from the thecorhiza. *U.Cam.*, USSR (Sib.).

**Galeograptus** Wiman, 1901, p. 189 [**G. wennersteni;* M]. Rhabdosome discoidal, erect portions of autothecae associated in comparatively few (8 to 10) peripheral branches bifurcating usually once near their mid-length; proximal autothecae with umbellate apertural processes; bithecae extending along the branches. *U.Ord.-M.Sil.(Wenlock)*, Baltic-Eng.——Fig. 29,2. **G. wennersteni,* lateral view of rhabdosome; silicified boulder, Sweden (Gotland); ×3 (267).

?**Parvitubus** Skevington, 1963, p. 47 [**Azygograptus? oelandicus* Bulman, 1936, p. 46; OD]. Erect, undivided branches comprising stolothecae, autothecae and bithecae, possibly grouped on a thecorhizal base; bithecae restricted to one side of stipe, opening into autothecae. *L.Ord.(Vaginatumkalk, Ontikan,* Sweden(Öland).——Fig. 30, *1-2.* **P. oelandicus* (Bulman); *1,* basal portion of stipe; *2,* distal portion of stipe [*a,* autothecae; *bi,* bithecae], ×7.5 (214).

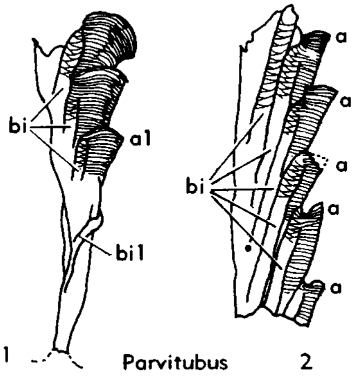

Fig. 30. Idiotubidae [*a,* autotheca; *bi,* bitheca] (p. *V*49).

# CAMAROIDEA

## Order CAMAROIDEA Kozłowski, 1938

[Introduced by Kozłowski in 1938 (p. 185) without diagnosis but descriptive notes in text; defined by Bulman (21) in 1938, p. 92, but first adequately described by Kozłowski (114) in 1949, p. 170]

Encrusting Graptolithina comprising autothecae and indistinct stolothecae, bithecae present in some; autothecae strongly differentiated into two parts, an inflated basal vesicle (camara) and a free tubular distal portion (collum); bithecae tubular; stolothecae forming bifurcating network above camarae or represented by extracamaral tissue surrounding stolons. *Ord.*

## MORPHOLOGY

The shape of the complete rhabdosome is unknown, as is its proximal end and mode of development. As in the Graptoloidea, the dominant element is the autotheca, but sclerotized stolons are present invariably, some enclosed in stolothecae, and bithecae characterize one genus.

### AUTOTHECAE

The autothecae are very sharply differentiated into distinct proximal and distal portions. The **camara** (proximal portion) is a more or less inflated vesicle or cell, whose upper wall exhibits characteristic fusellar structure in contrast to the lower surface which is structureless; the camarae, commonly embedded in extra-camaral tissue, form a sort of encrusting mosaic. At the proximal extremity of each is attached the autothecal stolon, separated from the cavity of the camara by one or more transverse partitions or septa. From one extremity also, although not necessarily the distal one, arises the slender tubular **collum,** which is morphologically equivalent to the free portion of the autothecae in the Tuboidea. Its wall shows a somewhat irregular fusellar structure and terminates in an apertural process (corresponding to the ventral process of Tuboidea and other graptolites) or more typically thins out distally to terminate in a sharp jagged edge; it has been suggested that this latter feature indicates a gradual transition in life from the sclerotized thecal wall into the soft skin of the zooid. Rarely (as in *Cysticamara accollis*). the collum is absent altogether and the thecal aperture is situated on the upper surface of the camara. Occlusion of the autothecae by a sclerotized diaphragm, generally near the base of the collum, is of very common occurrence.